OBJECT PERMANENCE IN ORANGUTANS, GORILLAS, AND BLACK-AND-WHITE RUFFED LEMURS

A Dissertation
Presented to
The Academic Faculty

By

Suma Mallavarapu

In Partial Fulfillment
Of the Requirements for the Degree
Doctor of Philosophy in Psychology

Georgia Institute of Technology

August, 2009

Object Permanence in Orangutans, Gorillas, and Black-and-White Ruffed Lemurs

Approved by:

Dr. Terry L. Maple, Advisor
School of Psychology
Georgia Institute of Technology

Dr. Tara S. Stoinski
School of Psychology
Georgia Institute of Technology

Dr. Fredda Blanchard-Fields
School of Psychology
Georgia Institute of Technology

Dr. Robert R. Hampton
Department of Psychology
Emory University

Dr. Marcus Jackson Marr
School of Psychology
Georgia Institute of Technology

Date Approved: April 28, 2009

ACKNOWLEDGEMENTS

I would like to thank my committee members, Drs. Terry Maple, Fredda Blanchard-Fields, Jack Marr, Tara Stoinski, and Robert Hampton for their invaluable advice and guidance over the past few years. Special thanks are due to my advisor, Terry Maple, who has always encouraged, inspired, and given me confidence in myself. I also owe a debt of gratitude to Bonnie Perdue, for helping in the data collection, for her patience in answering the countless questions that I had regarding the statistical analysis of the data, and for the time she made for our many talks which improved this project tremendously. Special thanks are due to Zoo Atlanta's primate care-staff, for making this project possible, and the Georgia Tech Center for Conservation and Behavior for providing excellent resources and opportunities for research and education.

I would like to recognize the financial support that made this work possible. My primary source of funding over the past few years has come from the Elizabeth Smithgall Watts Fellowship established at Zoo Atlanta, and from a Dissertation Year Award granted by the Southern Regional Education Board's Doctoral Scholars Program. A dissertation award awarded by the American Psychological Association also made this project possible.

Last, but not least, I thank my family and friends, especially my husband and my parents…this work would not have been possible without their constant love and support.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

SUMMARY

This study examined object permanence in Sumatran orangutans (*Pongo abelii*), Western lowland gorillas (*Gorilla gorilla gorilla*), and black-and-white-ruffed lemurs (*Varecia variegata)* at Zoo Atlanta. Object permanence has been defined as the understanding that objects continue to exist even they are not perceived-- when this understanding is fully developed, individuals are able to represent the unperceived trajectory of objects. Object permanence is necessary for many species to efficiently forage for hidden food and to locate moving prey, predators, or group members. Object permanence has been extensively studied in humans, as well as several non-human species: various primate species, dogs, cats, and birds.

A literature review reveals two main issues with object permanence research in non-human primates. One of the issues is that it is difficult to make valid comparisons between different species because very few studies have been conducted using appropriate controls. Thus, one of the goals of this study was to conduct control trials for all tasks in the traditional object permanence test battery, in order to reliably assess and compare performance in the species under study. The second issue is concerned with the finding that all of the non-human primate species tested so far have failed one of the more difficult tasks in the test battery, namely the non-adjacent double invisible displacement task. It has been hypothesized that this performance limitation is a result of the manner in which the task is presented. Thus, the second goal of this study was to modify the existing methodology and present the task to gorillas and orangutans in locomotive space

to see if performance improves. This is the first study to present this task to non-human primate species in locomotive space.

This study found that orangutans were the only species to reliably pass most tasks in the traditional object permanence test battery. Black-and-white ruffed lemurs failed most visible and invisible displacement tasks. Owing to the small sample size of gorillas in this study, further research is required before any firm conclusions can be made about the ability of this species to solve visible and invisible displacement tasks in the traditional object permanence test battery. Presenting the boxes in locomotive space to gorillas and orangutans did not improve performance on the non-adjacent double invisible displacement task. Further research is required to resolve the question of whether this performance limitation is a result of the manner in which the task was presented.

A third goal of this dissertation was to try and ensure that no simple search strategies could account for success in solving the tasks in the traditional test battery. Some previous studies have controlled for strategies such as "search in the last box visited by the experimenter" and "search in the first box visited by the experimenter." While the present study also controlled for these strategies, I found that subjects could appear to succeed on some tasks by using a strategy of "randomly choosing between the two boxes visited by the experimenter." This finding warrants a re-evaluation of object permanence in all species studied to date. Future studies of object permanence in non-human primates should test for this strategy as well.

CHAPTER 1

INTRODUCTION

Jean Piaget (1952, 1954) defined object permanence as the understanding that objects continue to exist even they are not perceived. He claimed that this understanding develops in stages in children during the first two years of life, and when this understanding is fully developed, children are able to represent the unperceived trajectory of objects.

According to Piaget, object permanence starts to develop when the infant is between 4 to 8 months of age, and is fully developed by the time the infant is between 18 to 24 months of age. Piaget divided the developmental process of object permanence itself into six stages. During the first two stages (birth to 4 months), human infants do not search for objects that have disappeared. During the third stage (4 to 8 months), infants can recover a partially occluded object, although there is no systematic search for completely hidden objects. During the fourth stage (8-12 months), they can recover a completely hidden object, but only if they start grasping at it at the time it disappears (Stage 4a); and later (Stage 4b), they can find a hidden object without the initial grasping motion. But infants commit the so-called "A-not-B error" (or perseveration error) by searching for the object in the location where it was previously retrieved from successfully.

During Stage 5 (12-18 months), infants no longer commit the A-not-B error (Stage 5a); they can also find an object that has been successively hidden behind different occluders within the same trial (Stage 5b). During Stage 6 (18-24 months), infants start solving invisible displacements (in which the movement of the object is not visible).

Piaget claimed that individuals who attain stage 4 understand that an object continues to exist even when it is not perceived; individuals who attain stage 5 are capable of tracking an object that is successively visibly displaced behind different occluders; and individuals who attain stage 6 are capable of representing the unperceived trajectory of an object.

Object Permanence Research in Humans

Piaget's stage theory was based on informal testing of his own children. Early researchers of object permanence in human infants standardized these informal tests (for instance, Gratch, 1977; Harris, 1975; Schuberth, 1983; Sophian, 1985; Sophian & Sage, 1983; Uzgiris & Hunt, 1975). These early studies usually involved hiding an object behind/under one of a few hiding locations (screens or boxes), and allowing infants to make a search response.

Using this method, researchers found evidence to support Piaget's stage theory of object permanence development. One of the main findings was in support of Piaget's claim that infants attain the fourth stage by about 9 months of age. But, results from the seminal study conducted by Baillargeon, Spelke, and Wasserman (1985) revealed that infants as young as 5 months of age might be attaining the fourth stage of object permanence. Baillargeon et al. (1985) argued that a Piagetian search task was too difficult for very young infants; instead of reflecting "limited competence" to solve stage 4 tasks, the difficulty of Piaget's tasks reflected "performance limitations" because of the need to coordinate separate actions toward separate objects (means-end sequences). That is, infants could not solve the tasks because they could not physically retrieve the object with the necessary coordinated limb movements (which apparently develop only when

infants have reached around 9 months of age). Thus, the experiments conducted by Baillargeon et al. (1985) used the violation-of-expectation (VOE) paradigm, which did not require infants to perform actions; it relied on looking-times, instead. Infants were habituated to a screen that rotated back and forth through a 180 degree arc. Then, a box was placed behind the screen, and the infants saw two events: 1. the screen rotated until it reached the hidden box, and then came back (expected event); 2. the screen rotated through a full 180 degree arc as though the box was absent (unexpected event). The infants looked longer at the unexpected event, which was taken to indicate that they possessed some understanding that objects continue to exist even when they cannot be perceived, and so were "surprised" at the unexpected event.

Researchers using the VOE paradigm have repeatedly found that infants as young as 3 to 4 months of age attain the fourth stage of object permanence (Aguiar & Baillargeon, 2002; Baillargeon, 1987; Baillargeon, 1993; Baillargeon & Graber, 1987; Kellman & Spelke, 1983; Luo, Baillargeon, Brueckner, Munakata, 2003; Ruffman, Slade, & Redman, 2005; Spelke, Breinlinger, Macomber, and Jacobson, 1992; Spelke & Hespos, 2001). However, this claim has been disputed by several researchers (Bogartz & Shinskey, 1998; Bogartz, Shinskey, & Speaker, 1997; Haith, 1988; Meltzoff & Moore, 1998; Moore & Meltzoff, 1999; Munakata, 2001; Munakata, McClelland, Johnson, & Siegler, 1997; Schlesinger & Casey, 2003; Thelen, Schoner, Scheier, & Smith, 2001).

More recently, some researchers have suggested that object permanence is innate (Baillargeon, 2008; Spelke, 2007), while others have argued that it is acquired over time (Cohen, Chaput, & Cashon, 2002; Mareschal, Johnson, Sirois, Spratling, Thomas, & Westermann, 2007). Other areas of recent research on object permanence in humans

include studies on variables (such as object boundaries and proximity relations) that affect children's search for hidden objects (Shutts, Keen, & Spelke, 2006), permanence for moving objects (Bremner, Johnson, Slater, Mason, Foster, Cheshire, & Spring, 2005), permanence for familiar versus novel objects (Shinskey & Munakata, 2005), infants' search for hidden persons (Krojgaard, 2005), and search for hidden objects in the dark (Shinskey, 2008; Shinskey & Munakata, 2003).

Object Permanence Research in Animals

Early researchers used tasks that were developed for human infants (for instance, Uzgiris & Hunt, 1975) to test for object permanence in animals. The tasks were modified, however, to suit the characteristics of different species. These early studies usually involved hiding an object behind/under one of two to five hiding locations (screens or boxes), and allowing the subject to make a search response. A series of visible and invisible search tasks were administered. *Visible tasks* are those in which the subject can see the movement of the object in between the hiding locations because the experimenter's open hand or a transparent "displacer" is used to move the object. *Invisible tasks* are those in which the subject *cannot* see the object moving in between the hiding locations because an *opaque displacer* is used to move the object. Visible and invisible tasks consist of either single displacements (in which the object is moved behind/under one hiding location, and left there), or double displacements (in which the object is moved behind/under two hiding locations in succession, before being left at the second location). Success on single visible displacement tasks is taken as evidence of an understanding that an object exists even when it is not perceived. Success on double

visible displacement tasks is taken as evidence of an ability to track a visibly moving object. Success on invisible displacement tasks is taken as evidence of an ability to represent the unperceived trajectory of an object.

Object Permanence Research in Birds, Cats, and Dogs

Using the method described above, researchers have found that the following non-primate species can solve *visible* displacement tasks: ring doves (Dumas & Wilkie, 1995), kakarikis (Funk, 1996), magpies (Pollok, Prior, & Gunturkun, 2000), domestic cats (Dore, 1986, 1990; Dumas, 1992; Dumas & Dore, 1989, 1991; Goulet, Dore, & Rosseau 1994), and dogs (Triana & Pasnak, 1981). It has also been found that visible *and* invisible displacement tasks can be solved by psittacine birds (Funk, 1996; Pepperberg & Funk, 1990; Pepperberg & Kozak, 1986, Pepperberg, Willner, & Gravitz, 1997). Until very recently, it was thought that dogs could also solve *invisible* displacements (Gagnon & Dore, 1992; 1993; 1994; Watson, Gergely, Csanyi, Topal, Gacsi, & Sarkozi, 2001). However, rigorously controlled studies on dogs by Collier-Baker, Davis, and Suddendorf (2004), and Fiset and LeBlanc (2007) have proved otherwise, thus calling into question the earlier results with psittacine birds too.

Object Permanence Research in Non-Human Primates

Formal research on object permanence in non-human primates began during the 1970s (see Tomasello & Call, 1997, for a review). Object permanence in non-human primates is studied under the realm of "physical cognition," which is a term that encompasses the ability to find objects in large-scale and small-scale space, and to manipulate, categorize,

and quantify objects (Tomasello & Call, 1997). Before describing previous research on object permanence in non-human primates, it is important to have a brief discussion about theories of physical cognition that attempt to explain how cognitive skills might have evolved in primates as adaptations to different ecological conditions. Two major theories that have been proposed in the context of foraging will be discussed in the next section, followed by a brief discussion of Tomasello and Call's (1997) extension of these theories to object permanence.

Theories of Primate Physical Cognition

Foraging theory. Milton (1981, 1988) suggested that the type of foraging behavior exhibited by primates depends on their diet, and that complex cognitive skills evolved because of foraging demands. She notes that plant foods are a major portion of the diet of all extant primates, and that plant foods are patchily (not uniformly) distributed in the environment both spatially and temporally, but with some degree of predictability (fruits are more patchily distributed than leaves; different types of fruits and leaves are available at different times of the year). The patchiness would make it difficult for a primate to specialize on only a few plant species, especially given the constraints of day-range sizes and energy requirements. Milton hypothesized that patchiness is equivalent to foraging complexity, and that the complexity of cognitive skills increases with an increase in foraging complexity, given that patchy resources are predictable. Thus, Milton hypothesized that many primates might have evolved complex cognitive skills to locate and identify food sources. Furthermore, since tropical forest environments may change quickly, it would be ideal if primates were born with flexible and adaptable learning

skills, instead of knowledge of different kinds of food. Milton suggested a correlation between a species' brain size (corrected for body size) and the patchiness of food resources that a species exploits, and found evidence to support this hypothesis by examining spider monkeys, a more frugivorous (primarily fruit-eating) species, and howler monkeys, a more folivorous (primarily leaf-eating) species. She found that the former had a larger brain size (corrected for body size) than the latter. Clutton-Brock and Harvey (1980) also found that frugivorous primates have larger brains (relative to body size) than folivorous primates.

Tomasello and Call (1997) describe a few problems that have been found with this theory. First, Byrne (1994) has argued that brain encephalization should be used as a measure of complex cognitive skills, instead of brain size, because body size is not relevant in this context. Second, Dunbar (1992, 1995) has argued against the use of day-range size as a measure of foraging complexity, because different species might find the same environment to be complex in different ways, depending on body size. When he corrected day-range size for body size, he did not find any correlation between the complexity of foraging demands and "intelligence" (as measured by neocortical expansion).

Extractive foraging theory. Parker and Gibson's (1971, 1979) theory focuses on "extractive foraging," which is the process by which an animal extracts food that is not easily accessible from a substrate or shell (for instance, opening nuts, digging for tubers, looking under bark or rocks for insects, and using tools to extract insects or honey). Since the food is not directly perceptible, and extracting it requires complex object manipulation skills, Parker and Gibson hypothesized that extractive foragers must have

evolved complex cognitive skills, including the capacity for mental representation, for this purpose. They found support for this hypothesis in the observation that omnivorous species that are extractive foragers, and that use tools either in the wild (such as chimpanzees and capuchin monkeys), or in captivity (such as gorillas and orangutans), score high on Piagetian scales of sensory-motor intelligence. One criticism of this theory is that although extractive foraging is widespread among other primate and non-primate species, it is not always correlated with high-level performance on Piagetian scales of sensory-motor intelligence (Tomasello & Call, 1997).

Theory for the evolution of object permanence skills. Tomasello and Call (1997) suggested that basic skills of object permanence, with which individuals understand that an object continues to exist even when it is not perceived, might have very well evolved within the context of foraging, including extractive foraging. However, they hypothesized that an ability to represent the unperceived movements of objects (stage 6 invisible displacements) might have evolved in species that need to track mobile prey, predators, or group members. Most primates live in social groups; many have predators and prey on mobile invertebrates. Thus, Tomasello and Call hypothesize that it is not likely that too many differences will be found within primate species, in the domain of physical cognition, in general, and object permanence skills, in particular. This hypothesis has been supported by research on the representational abilities in monkeys and apes (see Call, 2000, for a review).

Findings from Object Permanence Research on Non-Human Primates

Early studies found that many species of monkeys and apes were capable of solving both visible and invisible displacement tasks. These species included squirrel monkeys (Vaughter, Smotherman, & Ordy, 1972), rhesus monkeys (Wise, Wise, & Zimmerman, 1974), woolly monkeys (Mathieu, Bouchard, Granger, & Herscovitch, 1976), capuchin monkeys (Mathieu et al., 1976), stump-tailed macaques (Parker, 1977), gorillas (Redshaw, 1978), and chimpanzees (Mathieu et al., 1976; Mathieu & Bergeron, 1981; Wood, Moriarty, Gardner, & Gardner, 1980).

However, in a seminal paper that can be considered as a turning point in the history of the study of object permanence in non-human species, Natale, Antinucci, Spinozzi, and Poti (1986) argued that previous research on non-human primates could only provide evidence of an understanding that objects continue to exist when they are not perceived. It could not provide indisputable evidence of an ability to track a visibly moving object and to represent the unperceived trajectory of an object because the double visible and invisible tasks could be solved by using simple search strategies. For instance, Natale et al. (1986) claimed that because the object was always hidden in the last location visited by the experimenter, subjects could simply be using the rule "search in the last location visited," thereby solving the tasks. The authors designed suitable tasks to control for this search strategy, while administering single invisible displacements to a juvenile gorilla and a Japanese macaque. Their apparatus consisted of two large boxes (the bottom side of each box was open in order to hide a food reward). During regular trials, the reward was placed in a small box (the opaque displacer), which was then moved to under one of the large boxes. The reward was inconspicuously left under the large box (by tilting the large

box in such a way as to prevent the subjects from seeing the transfer), and the small box was then moved to a final location (to one end of the array of large boxes). However, the researchers also introduced some control trials in which, after placing the reward in the small box, this was not moved to under a large box. Instead, the experimenter just tilted one of the large boxes, as done in the regular trials. The study found that while both the gorilla and Japanese macaque solved the regular trials, only the gorilla passed the control trials (that is, the Japanese macaque searched under the large box that was tilted, even though it had never seen the small box with the reward move under it). The authors concluded that administering appropriate control trials was imperative to any study of object permanence, and suggested that previously studied species should be re-evaluated with this in mind.

Using the same procedure that Natale et al. (1986) developed, Schino, Spinozzi, and Berlinguer (1990) found that capuchin monkeys and long-tailed macaques could not solve control invisible displacement tasks. Since the early 1990s, researchers have used a slightly modified version of the tasks developed by Natale et al. (1986) to test for object permanence in various species of non-human primates. This modified version makes use of three boxes (labeled A, B, C), and a displacer (a transparent one for visible tasks, and an opaque one for invisible tasks) to displace a food reward. Some, or all, of the following tasks are administered[1] (Figure 1 depicts some of the tasks in this battery):

[1] Description of tests is adapted from de Blois, Novak, and Bond (1998). In all the tests described, after the reward is left in the final hiding place, the displacer is shown to be empty and moved away to a randomly pre-determined location (a spot on either side of the array of boxes, or a spot in between the boxes). Henceforth, these tests will be referred to as "regular tasks" to distinguish them from "control tasks."

Test 1: Single visible displacement. The reward is placed in a transparent displacer in full view of the subject. The displacer is then moved into one of the boxes, where the reward is left. The reward is hidden under the same box in all trials.

Test 2: Sequential visible displacement. After the last trial of test 1, the reward is hidden in a different box for a few trials (for instance, subjects that see the displacer being placed in box A in test 1, now see it being placed in box C, and vice versa).

Test 3: Alternate visible displacement. On each trial, the experimenter varies the location of the reward among boxes A, B, and C.

Test 4: Double visible displacement. Within a single trial, the displacer is moved into one box, removed, and then moved into a second box, where the reward is hidden.

Test 5: Triple visible displacement. Within a single trial, the displacer is moved into three boxes successively, and the reward is left under the third box.

Test 6: Single invisible displacement. The reward is placed in an opaque displacer in full view of the subject. The displacer is then moved into one of the boxes, where the reward is left. The reward is hidden under the same box in all trials.

Test 7: Sequential invisible displacement. After the last trial of test 6, the reward is hidden in a different box for a few trials, with the same procedure as in test 6 (for instance, subjects that see the displacer being placed in box A, now see it being placed in box C, and vice versa).

Test 8: Alternate invisible displacement. On each trial, the experimenter varies the location of the reward among boxes A, B, and C.

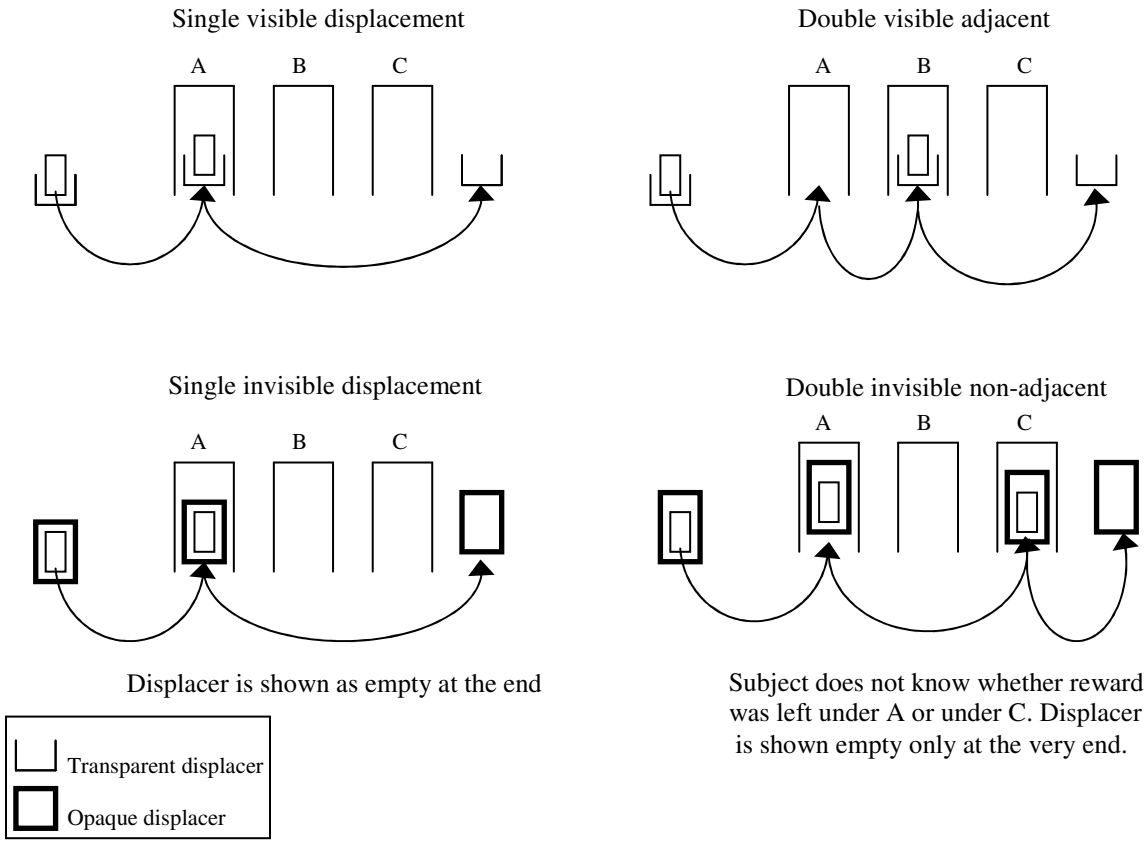

Figure 1. Depiction of some of the tasks in the battery.

Test 9: Double invisible displacement. Within a single trial, the displacer is moved into one box, removed, and then moved into a second box, where the reward is hidden (the displacer is not opened in between these two box visits). Then the displacer is removed, shown empty, and moved to a final pre-determined location (as in all the other tests). Subjects are given a second chance to look for the reward if their first choice involves the first box visited (but not baited) by the experimenter; if not, the trial ends at once (this is the only task in which subjects are allowed two chances).

Researchers administering this entire test battery have also used some control trials to control for the "search in the last location visited" strategy in the following species: rhesus monkeys (de Blois & Novak, 1994), orangutans (de Blois et al., 1998), cotton-top tamarins (Neiworth, Steinmark, Basile, Wonders, Steely, & DeHart, 2003), and common marmosets (Mendes & Huber, 2004). After administering all the *visible* tasks in the test battery, these researchers included some control trials in which: the reward is placed in a transparent displacer which is moved into one box, removed, and then moved into a second box, where the reward is hidden. After the displacer is shown empty, it is moved into a third box, before being placed in a final pre-determined location (this can be labeled as a *double visible displacement control* because the empty transparent displacer is moved into a *third* box, after the reward is hidden in the *second* box). Some of these researchers also included some control trials after administering all the *invisible* tasks in the test battery as follows:

1. The reward is placed in an opaque displacer which is moved into one box, removed, and then moved into a second box, where the reward is hidden. After the displacer is shown empty, it is moved into a third box, before being placed in a final pre-determined location (rhesus monkeys-- de Blois & Novak, 1994; marmosets-- Mendes & Huber, 2004). This can be labeled as a *double invisible displacement control* (see explanation above).
2. The reward is placed in an opaque displacer. The displacer is moved into one box where the reward is hidden. Then the displacer is shown empty and moved into a second box, before being placed in a final pre-determined location (orangutans-- de Blois et al., 1998; tamarins-- Neiworth et al., 2003). This can be labeled as a

single invisible displacement control because the empty opaque displacer is moved into a *second* box, after the reward is hidden in the *first* box.

Thus, a single block of control trials was administered for all visible tasks combined, as well as all invisible tasks combined, instead of control trials after each and every task in the test battery. Moreover, as can be seen from the above description, one kind of invisible displacement control was used in two studies, and another kind was used in the other two studies (as will be explained later, to make proper comparisons across species, it would be better to standardize the methodology in such a way as to administer control trials for each and every task in the battery, and to label each control task in the manner described above, to avoid any confusion).

The rhesus monkeys, orangutans, and tamarins tested with the test battery were found to successfully solve all *visible* tasks-- both regular and control trials (marmosets failed visible controls, but passed the regular trials).

Results were mixed when *invisible* tasks were considered: rhesus monkeys failed all invisible tasks, including controls (de Blois & Novak, 1994). Marmosets failed sequential and double invisible displacements, but passed single and alternate (Mendes & Huber, 2004). Neiworth et al. (2003) claimed that cotton-top tamarins solved all invisible tasks (except for the single invisible controls). However, owing to some methodological differences in their study (the displacer was opened in between box visits in their double invisible displacement task, thus rendering it a single displacement), other researchers have questioned the validity of these findings (for instance, Fedor, Skollar, Szerencsy, & Ujhelyi, 2008).

Orangutans solved all invisible tasks (including the single invisible controls), except for the double invisible displacements (de Blois et al., 1998). When analyzing double invisible displacements, the authors made a distinction between two types of displacements. In *adjacent* displacements, the displacer visits two adjacent boxes in succession (for instance, AB, BA, BC, CB), before being placed in its final position. In *non-adjacent* displacements, the displacer visits two non-adjacent boxes in succession (for instance AC or CA), before being placed in its final position. De Blois et al. (1998) found that orangutans passed the adjacent trials, but not the non-adjacent trials, which resulted in the overall finding of a failure in the double invisible displacement task.

Not all researchers have made use of all the tests in the battery described previously. Call (2001) used alternate visible, double visible, alternate invisible, and double invisible tasks to test for object permanence in orangutans and chimpanzees. He did not administer any control trials. However, the manner in which he conducted the double visible and double invisible tasks eliminated any need for controls for the *double* displacements. Unlike most other researchers who always left the reward under the *second* box visited during double displacements, Call *alternated* the hiding location between the first and second boxes visited. This not only controlled for the use of the strategy "search in the last location visited," but also controlled for the use of another strategy, namely "search in the first location visited." His study replicated the de Blois et al. (1998) finding—subjects passed all tasks except for non-adjacent double invisible displacement trials. Similar results were obtained in a study by Barth and Call (2006), who used single and double invisible displacements to test for object permanence in chimpanzees, bonobos, orangutans, and gorillas. All species solved all tasks, except for non-adjacent double

invisible displacement trials. As in Call (2001), the authors did not administer any control trials. However, as explained above, the manner in which they conducted the double invisible displacement tasks eliminated any need for controls for that task. Similar results were also obtained in a study by Collier-Baker and Suddendorf (2006), who used double invisible displacements to test for object permanence in chimpanzees in the same manner as Call (2001).

Another study in which all tasks were not used was conducted by Collier-Baker, Davis, Nielson, and Suddendorf (2006), who used single invisible displacements to test for object permanence in chimpanzees. They administered specific control trials to control for the use of both the "last location visited" and "first location visited" strategies, and found that their subjects successfully solved all control tasks.

In a more recent study, Fedor et al. (2008) tested various species of gibbons on single visible, single invisible, and double invisible tasks, using just single invisible controls. Owing to the high individual variability found across all tasks, and some evidence of the use of various search strategies, the authors cautioned that more studies need to be conducted before any conclusion can be drawn about gibbons as a species.

In sum, research to date indicates that visible displacement tasks with some form of control can be solved by two great ape species-- orangutans (Call, 2001; de Blois et al., 1998) and chimpanzees (Call, 2001), and two monkey species-- rhesus monkeys (de Blois & Novak, 1994) and cotton-top tamarins (Neiworth et al., 2003). Research also indicates that several invisible displacement tasks with some form of control can be solved by great apes (results are unclear in studies of monkeys): orangutans (Barth & Call, 2006; Call, 2001; de Blois et al., 1998), chimpanzees (Barth & Call, 2006; Call,

2001; Collier-Baker et al., 2006), and bonobos and gorillas (Barth & Call, 2006). However, using the methods described, no great ape species has been found to solve non-adjacent double invisible displacement trials (hypothesized reasons for failure will be discussed in detail in another section).

Although research on object permanence in non-human primates has come a long way, there is still a need for more studies to be conducted using monkeys, apes, and prosimians for the following reasons:

1. Very few studies using appropriate controls have been conducted (only one study with most species: bonobos, gibbons, gorillas, rhesus monkeys, and cotton-top tamarins; three studies with orangutans and chimpanzees)
2. Only four studies have used all the tasks in the test battery (de Blois & Novak, 1994; de Blois et al., 1998; Mendes & Huber, 2004; Neiworth et al., 2003). Gorillas, bonobos, and gibbons have never been tested on visible displacement tasks with suitable controls.
3. None of the studies conducted so far have used control trials for each and every task in the test battery, which is something that needs to be done in order to gain a more thorough understanding of object permanence in non-human primates, and in order to be able to make valid species comparisons (Collier-Baker et al., 2006).
4. Different studies have used different kinds of control trials, which makes it very difficult to draw valid species comparisons (that is, some studies have used only single invisible controls, while other studies have used only double invisible controls).

5. Although some studies have controlled for search strategies such as "last box visited" and "first box visited", researchers have admitted that subjects might be succeeding in some tasks by using yet other simple strategies (Collier-Baker et al., 2006; Fedor et al., 2008). If other strategies are found, it will warrant a re-evaluation of all species studied to date.

Thus, one of the goals of this dissertation was to test different primate species on all tasks in the object permanence test battery, using controls for every task in the battery (such a standardized methodology will yield valid species comparisons). Another goal was to ensure that no other simple search strategy could account for success in solving the tasks (please see next section for a description of one possible strategy that no other researchers seem to have taken into account).

Strategy of Randomly Choosing Between the Two Visited Boxes

In all the regular tasks of the test battery described in the previous section, the reward was always hidden in the last location visited by the experimenter. Thus, subjects could simply be using the rule-- "search in the last location visited," to solve the tasks. As described previously, an appropriate control for all the regular tasks in which a *single* displacement is made would be: move the displacer into one box where the reward is hidden, show the displacer as empty, and then move the empty displacer into a second box, before placing it in a final pre-determined location. This can be labeled as a *single displacement control* because the empty displacer is moved into a *second* box, after the reward is hidden in the *first* box (single *visible* displacement control if a *transparent* displacer is used, and single *invisible* displacement control if an *opaque* displacer is

used). If subjects pass *both* regular and control tasks, then it can be concluded that the tasks were solved without the use of the strategy "search in the last location visited."

For *single* displacements, previous researchers have analyzed both regular and control tasks as follows. The actual number of correct choices made by the subject was compared with the number expected if the subject were randomly choosing one box out of three (the probability of succeeding by doing this is 0.33). If there was no significant difference, then it was concluded that the subject failed the tasks. If the number of correct choices was significantly higher than the expected number (that is, if performance was "above chance"), then it was concluded that the subject passed the tasks (and in particular, solved the tasks without the use of a strategy of "search in the last location visited").

While this is an accurate method of analyzing performance on *regular* tasks (where one box is visited by the experimenter), I have found that the analysis for *control* tasks is incomplete (in control tasks for single displacements, *two* boxes are visited by the experimenter). In control tasks, if the number of correct choices is significantly higher than the number expected if the subject were randomly choosing one box out of three, we need to then verify whether the subject was using a strategy of *randomly choosing between the two boxes visited by the experimenter* (in which case, it might still appear that the subject is performing "above chance"). This can be done by comparing the number of choices to the baited box with the number of choices to the non-baited visited box (not using the total number of trials; only the number of trials on which the subject visited one of the two boxes in question; probability of chance success is then 0.5). If there is no significant difference, then it can be concluded that the subject has failed the

task. If there is a significant difference, then it can be concluded that the subject is not using the strategy of "randomly choosing one of the two boxes visited by the experimenter." Control trials for any *single* displacement task (i.e., single, sequential, and alternate *visible* controls, as well as single, sequential, and alternate *invisible* controls) need to be analyzed in this manner, as do the regular trials of the double visible displacement task (in which, the displacer is moved into one box, removed, and then moved into a second box, where the reward is hidden). This kind of analysis has not been conducted previously, and this is the first study to do so.

Hypothesized Reasons for Failure in Object Permanence Tasks

The main explanation that has been put forth for the finding that monkeys cannot solve invisible displacement tasks is that these species cannot represent the unperceived trajectory of an object, although they have some understanding that an object continues to exist in one location even if it cannot be seen (for instance, de Blois & Novak, 1994; de Blois et al., 1998; de Blois, Novak, & Bond, 1999).

The other failure that has been documented in object permanence studies has been the inability of all ape species to solve non-adjacent double invisible displacement trials. During the double invisible displacement task, an opaque displacer is moved into two boxes successively, and the reward is hidden under one of them (the displacer is not opened in between these two box visits). Then the displacer is removed, shown empty, and moved to a final pre-determined location. Subjects are given a second chance to look for the reward if their first choice involves a box visited, but not baited, by the

experimenter. Two kinds of displacements are possible: 1. Adjacent displacements, in which the displacer visits two adjacent boxes in succession (AB, BA, BC, CB), and 2. Non-adjacent displacements, in which the displacer visits two non-adjacent boxes in succession (AC or CA). Apes seem to be able to solve adjacent trials, but not non-adjacent, and the following hypotheses have been put forth to explain this finding:

1. Apes are capable of representing the unperceived trajectory of an object, but there are some limits to this capacity (Call, 2001).

2. The memory deficit hypothesis (de Blois & Novak, 1994; Gagnon & Dore, 1993): If the subjects' first choice involves the first box visited (but not baited) by the experimenter, then they are unable to remember which box was visited next, and so choose the center box. However, several studies have since ruled out this hypothesis as a possible explanation (Barth & Call, 2006; Call, 2001; de Blois et al., 1999).

3. The response bias-inhibition hypothesis (Call, 2001): Call found that the orangutans and chimpanzees he studied made second-choice errors as follows. If their first choice was to an unbaited visited box (which meant that they would have a second choice), they seemed unable to inhibit a response to the box right next to the one that they had just selected (the unbaited center box which was never visited by the experimenter). His subjects made a significantly greater percentage of second-choice errors in non-adjacent trials, when compared to adjacent trials. This finding led Call to hypothesize that apes have a bias towards searching in a sequence, with an inability to inhibit choosing the center box.

To further support his hypothesis, Call (2001) then administered some additional "no-displacement" trials in which he baited two boxes in full view of the subjects, closed

them, and then allowed the subjects to make a response. He presented adjacent and non-adjacent trials, both of which had two baited boxes, instead of the usual one baited box. Memory demands for both types of trials were thus the same. If the memory deficit hypothesis was correct, then subjects should have difficulties with both types of trials. However, Call found that subjects performed much better on adjacent trials. In non-adjacent trials, subjects again seemed unable to inhibit a response to the unbaited center box, after having selected one of the extreme boxes. That is, they had a tendency to uncover boxes sequentially on double displacements, which allowed them to solve adjacent, but not non-adjacent trials.

This brings us to one of the questions that researchers are currently trying to answer. Are apes capable of representing the unperceived trajectory of an object, but with some limits to this capacity? Or are these performance limitations a result of the manner in which the tasks are presented? Call (2001) hypothesized that arranging the boxes so close together in space might be causing the response bias of searching in a sequence, with an inability to inhibit choosing the center box. He suggested presenting tasks in a locomotive (not a small-scale) space, because having to move from one location to another might introduce costs associated with traveling and may reduce the tendency to search in locations that have not been visited by the experimenter (that is, the center box). If apes succeed on non-adjacent double invisible displacement trials in locomotive space, it would confirm that they are indeed fully capable of representing the unperceived trajectory of an object.

Thus, another goal of this dissertation was to present double displacement tasks to gorillas and orangutans in a locomotive space, to see if they could solve non-adjacent

double invisible displacement trials.[2] I also wanted to see if I could find support for Call's (2001) response-bias inhibition hypothesis by analyzing the different types of successes and errors on double invisible displacements.

Present Study

Justification for Choice of Species

As mentioned previously, basic skills of object permanence (with which individuals understand that an object continues to exist even when it is not perceived), might have evolved within the context of foraging and extractive foraging, and the ability to represent the unperceived movements of objects might have evolved in species that need to track mobile prey, predators, or group members. Since most primates need to track group members, and have to forage for plant food that remains at certain a location even when it is not being perceived, it has been hypothesized that not too many differences will be found within primate species in terms of representational skills (Tomasello & Call, 1997), and this hypothesis has been supported by findings from several studies, at least, studies of monkeys and apes (see Call, 2000, for a review).

In order to further test this hypothesis, I chose to study species from the three major groups of primates: black-and-white ruffed lemurs and ring-tailed lemurs (prosimians), Western lowland gorillas and Sumatran orangutans (great apes), and golden lion tamarins (a New World monkey species). These seemed to be suitable study species because all of them feed on plant foods to some extent. Gorillas are folivorous, but engage in seasonal frugivory (Doran & McNeilage, 2001). Orangutans and black-and-white ruffed lemurs

[2] Tests in locomotive space were not planned for the lemurs and golden lion tamarins because their enclosures were not suited for the method used.

are mainly frugivores (Cawthon Lang, 2005; Vasey, 2003). Golden lion tamarins and ring-tailed lemurs are omnivores, with fruit comprising a major portion of their diet; the latter feed on leaves as well (Kinzey, 1997; Sauther, Sussman, & Gould, 1999).

All five species also need to keep track of moving group members. Ring-tailed lemurs, black-and-white ruffed lemurs, gorillas, and golden lion tamarins live in social groups in the wild (Baker, Bales, & Dietz, 2002; Doran & McNeilage, 2001; Vasey, 2003; Watts, 1996); orangutans in the wild interact socially during breeding and when taking care of offspring (MacKinnon, 1974; Maple, 1980).

As a final note, at the time of this study, there had been no previous research conducted on object permanence in golden lion tamarins, ring-tailed lemurs, and black-and-white ruffed lemurs, and one of the aims of this study was to fill this gap in the literature.

Goals of this Dissertation

1. Test different primate species (orangutans, gorillas, golden lion tamarins, ring-tailed lemurs, and black-and-white ruffed lemurs) on all tasks in the traditional object permanence test battery, using controls for every task in the battery. This is the first study to conduct control trials for all tasks in the battery, and will thus aid in a more thorough evaluation of object permanence in the species under study (although properly analyzed control tasks are the only valid indicators of fully-developed object permanence as discussed in this introduction, I conducted regular trials as well, for comparison with previous research).

2. Ensure that no other simple search strategy can account for success in solving the tasks in the traditional test battery (to my knowledge, this is the first study to conduct a complete analysis to check for this).

3. Present double displacement tasks to gorillas and orangutans in a locomotive space, to see if they can solve non-adjacent double invisible displacement trials (this is the first study to present these tests in a locomotive space to non-human primate species).

4. See if I can find support for Call's (2001) response-bias inhibition hypothesis by analyzing the different types of successes and errors on double invisible displacements.

Hypotheses Tested

1. All species tested with the *traditional linear arrangement* will perform above chance on all visible and invisible tasks, except for the non-adjacent double invisible displacements.

2. All species tested with the *traditional linear arrangement* will make a significantly greater percentage of second-choice errors on non-adjacent double invisible displacement trials, when compared to adjacent trials.

3. The gorillas and orangutans tested with the arrangement in *locomotive space* will perform above chance on non-adjacent double invisible displacements (as hypothesized by Call, 2001).

4. All species will distinguish between the two boxes visited by the experimenter on all tasks requiring two displacements, when tested with either arrangement (that is, they will choose the baited box a significantly greater number of times than the unbaited, visited box).

CHAPTER 2

METHODS

Subjects

Subjects were housed at Zoo Atlanta during this study. Data could not be collected on two of the five species: the ten golden lion tamarins could not be habituated to the apparatus, and the four ring-tailed lemurs could not be separated into individual enclosures for testing. Data were collected on seven Sumatran orangutans (*Pongo abelii*), two western lowland gorillas (*Gorilla gorilla gorilla*), and five black-and-white ruffed lemurs (*Varecia variegata*). All subjects were adult animals. Subjects were tested individually, in their indoor enclosures. They were fed according to their normal daily routine. Water was available ad libitum. Subjects were not deprived of food or water during testing. One of the Sumatran orangutans (Chantek) had extensive experience with humans from an early age (Miles, 1990, 1994).

Procedure

The study consisted of two phases-- one using the traditional linear methodology, and the other using locomotive space as per Call's (2001) suggestion. During the first phase, there was a pretest period, during which the subjects were given a chance to become familiar with the testing situation and apparatus, and the subjects' ability to point to their chosen box was evaluated.

Phase I

Apparatus

The apparatus consisted of three opaque wooden boxes. The back-side of each box was open in order to hide the reward. The boxes were placed in a row (with some space in between the boxes) on a wooden rectangular platform (see Figure 2 below; X represents the subject behind the barrier; E represents the experimenter; the three boxes are labeled as A, B, and C, in order, from left to right). A transparent displacer was used during visible displacement trials and an opaque one was used during invisible displacement trials. Rewards used were grapes, raisins, peanuts, and apple pieces (depending on subjects' preference).

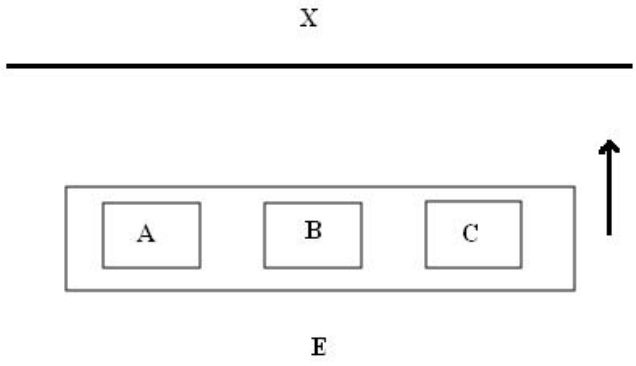

Figure 2. Linear Arrangement.

Pretest

During the pretest, the boxes were placed on the platform in such a way that the subject could see that they were empty (the open side of the boxes faced the subject). The experimenter (E) sat facing the subject behind the platform, placed a reward in one of the boxes in full-view of the subject, and then overturned all the boxes so that the subject

could not see the reward anymore. E then pushed the platform against the enclosure and the subject was allowed to select one of the boxes. If the subject selected the baited box, he/she received the food reward. If the subject selected the unbaited box, he/she was simply shown the empty box, and the experimenter retrieved the reward out of view of the subject, before moving on to the next trial. Subjects received six trials presented in a single session.

All the gorillas and orangutans at Zoo Atlanta understand "pointing" and were able to unambiguously point with their fingers to their chosen box (if they could reach the box, they would even touch their chosen box with one or more fingers). The lemurs had to be trained to point with their noses using a basic shaping procedure. On average, it took three 15 minute sessions to train each lemur to unambiguously point to one box out of an array of three (upon the prompt "where is it?"). "It" refers to the reward. The shaping procedure in no way resembled the procedure for the actual tasks. Rewards were not moved and hidden for them to find in a way that would have been done during testing. All three boxes were baited on every trial during shaping, and baiting was done without subjects' attention being drawn to the baiting.

Test

During the test, the boxes were placed on the platform in such a way that the subject could not see inside of them (the open side of the boxes faced the experimenter). During *visible* displacements, the experimenter placed the reward in the *transparent* displacer in full view of the subject, and performed the displacements by moving it above the board, and finally placing the reward in a randomly pre-determined box (this is a box that was

selected randomly prior to testing). After the reward was placed inside the box, the displacer was removed and shown to be empty to the subject. After the displacements were completed, the board was pushed towards the subject so that he or she could make a response. During *invisible* displacements, the same procedure was followed, except that the reward was first placed in the *opaque* displacer and then transferred to a randomly pre-determined box. The following tests were administered:[3]

Test 1: Single visible displacement. The reward was placed in the transparent displacer in full view of the subject. The displacer was then moved into one of the boxes, where the reward was left. The reward was hidden under the same box on all trials. Subjects were randomly assigned to groups that differed in which boxes were used for hiding (for instance, for the two gorilla subjects, one saw the experimenter place the reward in box A, and the other saw the experimenter place the reward in box C).

Test 2: Sequential visible displacement. After the last trial of test 1, the reward was hidden in a different box for a few trials. That is, subjects that saw the reward being placed in box A in test 1, now saw the reward being placed in box C, and vice versa.

Test 3: Alternate single visible displacement. On each trial, the experimenter varied the location of the reward among boxes A, B, and C.

Note: For some of the subjects, control trials were presented during each of the three tasks mentioned above, in which the empty displacer was moved into a second box, after the reward was dropped into the first box visited. This controlled for the use of the strategy "search in the last location visited."

[3] In all the tests described, after the displacer was removed from the last box visited, it was shown to be empty and moved away to a randomly pre-determined location (a spot on either side of the array of boxes, or a spot in between the boxes).

Test 4: Double visible displacement. Within a single trial the displacer was moved into one box, removed, and then moved into a second box, where the reward was hidden. The succession of boxes visited was randomly pre-determined. Some control trials were presented, in which the empty displacer was moved into a third box, after the reward was dropped into the second box visited. This controlled for the use of the strategy "search in the last location visited."

Test 5: Single invisible displacement. The reward was placed in the opaque displacer in full view of the subject. The displacer was then moved into one of the boxes, where the reward was left. The reward was hidden under the same box on all trials. Subjects were randomly assigned to groups that differed in which boxes were used for hiding.

Test 6: Sequential invisible displacement. After the last trial of test 5, the reward was hidden in a different box for a few trials, with the same procedure as in test 5. That is, subjects that saw the displacer being placed in box A in test 5, now saw the displacer being placed in box C, and vice versa.

Test 7: Alternate single invisible displacement. On each trial, the experimenter varied the location of the reward among boxes A, B, and C.

Note: For some of the subjects, control trials were presented during tests 5, 6, and 7, in which the empty displacer was moved into a second box, after the reward was dropped into the first box visited. This controlled for the use of the strategy "search in the last location visited."

Test 8: Double invisible displacement. Within a single trial the displacer was moved into one box, removed, and then moved into a second box. The reward was left in either one of those boxes. The succession of boxes visited was randomly pre-determined. Some

control trials were presented, in which the empty displacer was moved into a third box, after being shown as empty. Subjects were given a second chance to look for the reward if their first choice involved a "relevant" box (if not, the trial ended at once). A relevant box in a double invisible *regular* trial is one which the experimenter visited but did not bait. A relevant box in a double invisible *control* trial is one which the full displacer went into, but not where the reward was left.

These tests were given to each subject over the course of anywhere from 2 to 10 sessions (depending on how quickly the subject went through the tasks). Each testing session lasted anywhere from 5 minutes to 1 hour, depending on subjects' attention. Not all tests could be administered to all subjects because some subjects refused to participate after some time elapsed during each testing session (please refer to the tables for the number of subjects per test). For the same reason, the total number of trials per task varied (as can be seen in the tables). On tests 1 to 7, if the subject chose the baited box as a first response, E lifted the chosen box, thus revealing the reward and allowing the subject to retrieve it (or giving the subject the reward). If the subject touched an unbaited box, E showed the box as empty, retrieved the reward out of view of the subject, and then went on to the next trial. If the subject did not make a response within 15 seconds after the board was moved towards the enclosure, E retrieved the reward out of view of the subject and repeated the trial (after making sure the subject was paying attention). The flowchart on the next page (Figure 3) shows the procedure for test 8 (in the flowchart, "relevant box" refers to a box visited by the experimenter; it could be baited or unbaited).

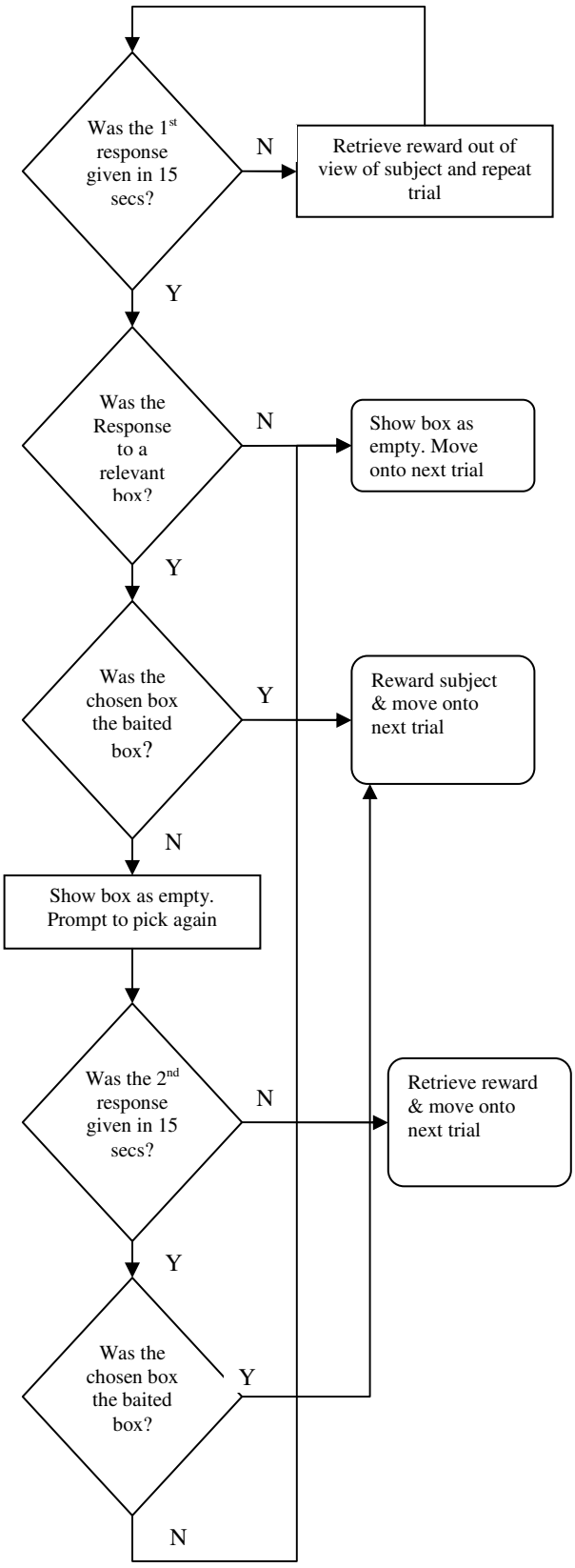

Figure 3. Flowchart detailing steps in test 8.

Phase II

Apparatus

The apparatus consisted of three remote-controlled cars; an overturned cardboard box was attached to the top of each car in order to make a flat platform on which each wooden box could be placed to hide the reward. The cars were placed about a foot away from the enclosure, and several feet away from each other. After the displacements were completed, the cars were simultaneously moved towards the subjects so that they could make a response. This set-up created a presentation of boxes in locomotive space (in double invisible displacements, once the subjects chose a visited but unbaited box, they needed to walk over to another box to make their second response). The same displacers and rewards that were used in Phase I were used in Phase II. The cars could not be used in the lemur enclosures because of space limitations, and so only gorillas and orangutans were tested in Phase II.

Test

During testing, double invisible displacements were performed as described previously, with the exception that in Phase II, the experimenter had to move around to complete the displacements (instead of sitting in front of the subject and completing the displacements over a smaller space). Four orangutans and two gorillas were tested. As in Phase I, the number of trials that could be administered depended on subject motivation to participate. Each orangutan received an average of 17 trials, and each gorilla received an average of 24 trials.

Standardized Protocol Used for all Tests in Both Phases

1. Trials in which the subjects were not paying attention to the displacements were stopped, and the trial was presented again. Test sessions were terminated and continued on another day if the subjects continued to be "inattentive" or "unmotivated." Subjects were considered to be inattentive or unmotivated if they failed to make a response within 15 seconds on five consecutive trials, turned gaze/body away from the apparatus before the displacements were completed, or started manipulating other objects in the enclosure and did not come back to the testing apparatus even after being called repeatedly, or shown a food reward.

2. This was a double blind study. I was one of the experimenters; I would sit in front of the apparatus, call for attention, perform the displacements, make sure the subject was attending to the entire displacement trajectory, bait a box, lower my head, close my eyes, and push the board towards the subject, while saying "where is it?" The second experimenter stood a little distance away. She would avert her gaze until I said "where is it?" and then quickly look to note the subject's response. We made sure that she did not see which box was being baited, and that I did not see which box was being chosen. When the second experimenter called out the chosen box, I would look up, show the subject what was under the chosen box, and if it was the correct box, I would give the subject the reward. If the subject touched the incorrect box, I showed the box as empty, retrieved the reward out of view of the subject, and then went on to the next trial. Phase 2 required a slightly different approach. After baiting a box, I would walk away with my face averted, saying "where is it?" The second experimenter would then use the remote control to move the cars forward so that the subject could make a response. The second

experimenter would then call out the chosen box, and I would walk back to either show the subject an empty box (if an incorrect response was made) or to reward the subject (if a correct response was made).

3. I made sure that there were no auditory cues by covering part of the board with a soft cloth that muffled any sound that the dropping of the reward might have caused. Both experimenters wore hats during all the sessions to prevent inadvertent gaze cues.

4. The following randomizations were incorporated into the procedure:

a. The initial and final positions of the displacer were randomized across trials (it could occupy either the terminal positions or the positions in-between the boxes).

b. The order of boxes visited by the experimenter was randomly pre-determined.

c. The final location of the reward was randomly pre-determined for every trial on alternate and double displacements.

e. The invisible and visible displacement tasks were counterbalanced to make sure that performance on one kind of task was not affected just because subjects were already exposed to the other. In this context, counterbalancing refers to the random assignment of subjects to two groups that differed in the order of presentation of visible and invisible displacement tasks

5. There were two types of double displacement trials: 1. Adjacent trials in which the displacer visited two adjacent boxes; and 2. Non-adjacent trials in which the displacer visited two non-adjacent boxes.

Data Analysis

The binomial test was used to analyze group performance on each task, wherein I compared observed number of successes with the number expected if the subject was responding completely randomly.

To analyze single displacement *regular* tasks (single, sequential, and alternate visible, as well as single, sequential, and alternate invisible), the actual number of correct choices was compared with the number expected if the subjects were randomly choosing one box out of three (the probability of succeeding by doing this is 0.33). If there was no significant difference, then it was concluded that the subjects failed the task. If there was a significant difference, then I verified whether subjects used a strategy of "search in the last location visited," by analyzing *control* trials.

Controls for single displacement tasks (single, sequential, and alternate visible displacements, *and* single, sequential, and alternate invisible displacements) were analyzed as follows:

1. The actual number of correct choices made by the subjects was compared with the number expected if the subjects were randomly choosing one box out of three (the probability of succeeding by doing this is 0.33). If there was no significant difference, then it was concluded that the subjects failed the task, and no further analysis was conducted.
2. If the number of correct choices was significantly higher than the expected number, then the strategy of "search in the *last* location visited" was eliminated. I then verified whether the subjects were using a strategy of randomly choosing between the two boxes visited by the experimenter (the probability of succeeding

by doing this is 0.5). This was done by comparing the number of choices to the baited box with the number of choices to the non-baited visited box (not using the total number of trials; only the number of trials on which subjects visited one of the two boxes in question). If there was no significant difference, then it was concluded that the subjects failed the task, because they were not distinguishing between the two boxes visited by the experimenter. If the number of choices to the baited box was significantly higher than to the unbaited visited box, then it was concluded that the subjects were not using the strategy of "randomly choosing between the two boxes visited by the experimenter" (however, subjects might still be using the strategy of "search in the *first* location visited," and analysis of the double visible displacement regular task is required to eliminate possible use of this strategy).

Regular double visible displacements were analyzed in a similar manner:

1. The actual number of correct choices made by the subjects was compared with the number expected if the subject were randomly choosing one box out of three (the probability of succeeding by doing this is 0.33). If there was no significant difference, then it was concluded that the subjects failed the task, and no further analysis was conducted.
2. If the number of correct choices was significantly higher than the expected number, then the strategy of "search in the *first* location visited" was eliminated. I then verified whether the subjects were using a strategy of randomly choosing between the two boxes visited by the experimenter (the probability of succeeding

by doing this is 0.5). This was done by comparing the number of choices to the baited box with the number of choices to the non-baited visited box (not using the total number of trials; only the number of trials on which subjects visited one of the two boxes in question). If there was no significant difference, then it was concluded that the subjects failed the task, because they were not distinguishing between the two boxes visited by the experimenter. If the number of choices to the baited box was significantly higher than to the unbaited visited box, then it was concluded that the subjects were not using the strategy of "randomly choosing between the two boxes visited by the experimenter."

If all known possible search strategies were eliminated when analyzing the double visible displacement task, as well as *controls* for single visible displacement tasks, then it was concluded that subjects were successful on visible displacements. Success on double visible *controls* will further strengthen this conclusion.

To analyze double visible *controls*, the actual number of correct choices was compared with the number expected if the subjects were randomly choosing one box out of three (the probability of succeeding by doing this is 0.33). If there was no significant difference, then it was concluded that the subjects failed the task. If there was a significant difference, then it was concluded that subjects solved the task without the use of either strategy ("search in the last location visited" or "search in the first location visited"). In these control tasks, because three boxes are visited, the question of the strategy of "randomly choosing between the two boxes visited by the experimenter" does not arise.

In double invisible regular and control trials (in which the reward can be placed in either one of the first two boxes visited by the experimenter), subjects were given a second chance to look for the reward if their first choice involved a box visited (but not baited) by the experimenter (after the subject's first choice, all three boxes were still available to the subject). Thus, the probability of succeeding by chance in these trials was 1/2. This is because there are two ways of succeeding on a trial:

1. The subject could succeed (in the first choice itself) by randomly choosing one of the three boxes (probability of which is 1/3).

OR

2. The subject could first pick the relevant box[4] (probability of doing this is 1/3), and then pick the baited box when given the second chance (probability of doing this is 1/2 because the subject is now choosing between the two remaining boxes). Thus, the overall probability of this type of second-choice success is (1/3) * (1/2), which is 1/6.

The combined probability of either of these events occurring is (1/3) + (1/6), which is 1/2. This is the probability of chance success in double invisible regular and control trials. If subjects performed significantly above chance on double invisible regular trials, then it was concluded that they solved these trials without the use of either strategy ("search in the last location visited" or "search in the first location visited"). However, we cannot rule out the possibility that they are using the strategy of "randomly choosing between the two boxes visited by the experimenter," unless this strategy was eliminated when

[4] A relevant box in a double invisible *regular* trial is one which the experimenter visited but did not bait. A relevant box in a double invisible *control* trial is one which the full displacer went into, but not where the reward was left.

analyzing *controls* for single invisible displacement tasks. If it was, then we can conclude that subjects were successful on invisible displacements.

If subjects performed significantly above chance on double invisible *control* trials, then it was concluded that subjects solved these trials without the use of either strategy ("search in the last location visited" or "search in the first location visited"). In these control tasks, because three boxes are visited, the question of the strategy of "randomly choosing between the two boxes visited by the experimenter" does not arise.

I also calculated the percentages of the following different types of successes and errors in adjacent and non-adjacent double invisible displacement trials (I compared the percentage of first-choice errors in adjacent and non-adjacent trials, as well as the percentage of second-choice errors in adjacent and non-adjacent trials using Wilcoxon signed ranks exact tests):

1. First-choice successes occur if a subject chooses the baited box on the first attempt.
2. First-choice errors occur if a subject chooses a non-baited, non-visited box on the first attempt.
3. Second-choice successes occur if a subject chooses the visited, non-baited box on the first attempt, and the baited box on the second attempt.
4. Second-choice errors occur if a subject chooses the visited, non-baited box on the first attempt, and the non-visited box on the second attempt.

CHAPTER 3

ORANGUTANS: RESULTS AND DISCUSSION

Pretest

All the orangutans were able to unambiguously point with their fingers to their chosen box (if they could reach the box, they would even touch their chosen box with one or more fingers).

Phase I

Visible Displacement Tasks

Orangutans performed above chance[5] on single, sequential, and alternate visible displacement *regular* tasks (binomial distribution, $p < 0.05$). Orangutans also performed above chance on single and sequential visible displacement *control* tasks (binomial distribution, $p < 0.05$). Further analysis[6] showed that there was a significant difference between the number of choices to the baited box and the number of choices to the unbaited visited box on single and sequential visible controls (binomial distribution, $p < 0.05$). Orangutans did not perform above chance on the alternate visible displacement *control* task (binomial distribution, $p > 0.05$).

[5] For the rest of the document, "performing above chance" means that the actual number of correct choices made by the subjects was significantly greater than the number expected if the subjects were randomly choosing one box out of three (the probability of succeeding by doing this is 0.33). This applies for all tasks, except for double invisible displacements, in which case, probability of chance success is 0.5.

[6] For the rest of the document "further analysis" means that I checked whether the subjects were using a strategy of randomly choosing between the two boxes visited by the experimenter (the probability of succeeding by doing this is 0.5). This was done by comparing the number of choices to the baited box with the number of choices to the non-baited visited box (not using the total number of trials; only the number of trials on which subjects visited one of the two boxes in question).

Orangutans performed above chance on the double visible displacement regular task (binomial distribution, $p < 0.05$). Further analysis showed that there was a significant difference between the number of choices to the baited box and the number of choices to the unbaited visited box on these displacements (binomial distribution, $p < 0.05$).

Double visible displacements were divided into adjacent and non-adjacent trials. Orangutans performed above chance on adjacent trials (binomial distribution, $p < 0.05$), and further analysis showed that there was a significant difference between the number of choices to the baited box and the number of choices to the unbaited visited box for these trials (binomial distribution, $p < 0.05$). Orangutans did not perform above chance on non-adjacent double visible displacements (binomial distribution, $p > 0.05$).

Post-hoc analysis showed that on the double visible non-adjacent trials, the number of choices to the irrelevant center box were significantly more than the number of choices to the visited but unbaited box (binomial distribution, $p < 0.05$).

Orangutans performed above chance on double visible displacement controls (binomial distribution, $p = 0.05$).

Please refer to Table 1 for a summary of orangutan performance on visible displacement tasks in Phase I.

Table 1. Orangutan Performance on Visible Displacement Tasks in Phase I.

		No. of subjects	No. correct	Total no. of trials	Percent correct	Above chance?[a]	Distinguished between the two visited boxes?[b]	Passed task?[c]
Regular								
	Single	6	37	52	71.2	Yes	--	Yes
	Sequential	6	47	56	84	Yes	--	Yes
	Alternate	5	47	72	65.3	Yes	--	Yes
	Double	5	34	70	48.6	Yes	Yes	Yes
	Double adjacent	5	22	35	62.9	Yes	Yes	Yes
	Double non-adjacent	5	12	35	34.3	No	--	No
Control								
	Single	6	20	31	64.5	Yes	Yes	Yes
	Sequential	2	8	9	88.9	Yes	Yes	Yes
	Alternate	2	6	17	35.3	No	--	No
	Double	5	15	31	48.4	Yes	--	Yes

Note. Dashes indicate that it was not necessary to check whether subjects were using the strategy of "randomly choosing between the two boxes visited by the experimenter," because it was either not applicable (that is, for single, sequential, and alternate regular trials, and double visible controls), or because subjects did not perform above chance (for instance, double visible non-adjacent trials and alternate controls).

Table 1 (continued)

[a] A "yes" in this column means that the actual number of correct choices made by the subjects was significantly greater than the number expected if the subjects were randomly choosing one box out of three (the probability of succeeding by doing this is 0.33), according to the binomial distribution (alpha = 0.05).

[b] A "yes" in this column means that the subjects were not using the strategy of "randomly choosing between the two boxes visited by the experimenter." The number of choices to the baited box was significantly greater than the number of choices to the non-baited visited box, according to the binomial distribution (alpha = 0.05).

[c] A "yes" in this column means that all possible strategies have been eliminated. This varies from task to task. A "no" means that subjects either did not perform above chance, or performed above chance, but did not distinguish between the two visited boxes. Please refer to the Data Analysis section in Chapter 2 for more details.

Invisible Displacement Tasks

Orangutans performed above chance on the single, sequential, and alternate invisible displacement *regular* tasks (binomial distribution, $p < 0.05$). Orangutans also performed above chance on single and sequential invisible displacement *control* tasks (binomial distribution, $p < 0.05$). Further analysis showed that there was a significant difference between the number of choices to the baited box and the number of choices to the unbaited visited box on single and sequential invisible controls (binomial distribution, $p < 0.05$). Orangutans did not perform above chance on the alternate invisible displacement control task (binomial distribution, $p > 0.05$).

Orangutans performed above chance on the double invisible displacement (binomial distribution, $p < 0.05$). This task was divided into adjacent and non-adjacent trials. Orangutans performed above chance on adjacent (binomial distribution, $p < 0.05$), but not on non-adjacent (binomial distribution, $p > 0.05$) double invisible displacements. Orangutans did not perform above chance on double invisible displacement controls (binomial distribution, $p > 0.05$).

Please refer to Table 2 for a summary of orangutan performance on invisible displacement tasks in Phase I.

Table 2. Orangutan Performance on Invisible Displacement Tasks in Phase I.

		No. of subjects	No. correct	Total no. of trials	Percent correct	Above chance?[a]	Distinguished between the two visited boxes?[b]	Passed task?[c]
Regular								
	Single	6	26	30	86.7	Yes	--	Yes
	Sequential	6	28	44	63.6	Yes	--	Yes
	Alternate	6	40	59	67.8	Yes	--	Yes
	Double	5	43	65	66.2	Yes	--	Yes
	Double adjacent	5	29	34	85.3	Yes	--	Yes
	Double non-adjacent	5	14	31	45.2	No	--	No
Control								
	Single	6	23	25	92	Yes	Yes	Yes
	Sequential	2	5	5	100	Yes	Yes	Yes
	Alternate	2	6	12	50	No	--	No
	Double	5	12	24	50	No	--	No

Note. Dashes indicate that it was not necessary to check whether subjects were using the strategy of "randomly choosing between the two boxes visited by the experimenter," because it was either not applicable (that is, for single, sequential, alternate, and double regular trials, and double invisible controls), or because subjects did not perform above chance (for instance, alternate controls).

Table 2 (continued)

[a] A "yes" in this column means that the actual number of correct choices made by the subjects was significantly greater than the number expected if the subjects were randomly choosing one box out of three (the probability of succeeding by doing this is 0.33), according to the binomial distribution (alpha = 0.05). This applies for all tasks, except for double invisible displacements (including adjacent, non-adjacent, and control trials), in which case, probability of chance success is 0.5.

[b] A "yes" in this column means that the subjects were not using the strategy of "randomly choosing between the two boxes visited by the experimenter." The number of choices to the baited box was significantly greater than the number of choices to the non-baited visited box, according to the binomial distribution (alpha = 0.05).

[c] A "yes" in this column means that all possible strategies have been eliminated. This varies from task to task. A "no" means that subjects either did not perform above chance, or performed above chance, but did not distinguish between the two visited boxes. Please refer to the Data Analysis section in Chapter 2 for more details.

I also calculated the percentages of the different types of errors and successes in adjacent and non-adjacent double invisible displacement trials (see Table 3). The sample size was too low to run a Wilcoxon signed ranks exact test to compare the percentage of second-choice errors in adjacent and non-adjacent trials. Post-hoc analysis showed that there was no significant difference between the percentage of first-choice errors in non-adjacent and adjacent trials (Wilcoxon signed ranks exact test: Total N = 5; ties = 0; ns).

Table 3. Mean Percentage of First- and Second-Choice Successes and Errors for Orangutans in Double Invisible Displacements in Phase I.

	First choice		Second choice	
Type of displacement	Success	Error	Success	Error
Adjacent	45.5	14.5	37.5	2.5
Non-adjacent	44.2	48.3	0	7.5

Phase II

Only regular double invisible displacements were administered in this phase. Orangutans performed above chance on the double invisible displacement task (binomial distribution, $p < 0.05$). This task was divided into adjacent and non-adjacent trials. Orangutans performed above chance on adjacent (binomial distribution, $p < 0.05$), but not on non-adjacent (binomial distribution, $p > 0.05$) double invisible displacements.

Please refer to Table 4 for a summary of orangutan performance on double invisible displacements in Phase II.

Table 4. Orangutan Performance on Double Invisible Displacements in Phase II.

		No. of subjects	No. correct	Total no. of trials	Percent correct	Above chance?[a]
Invisible						
	Double	4	50	71	70.4	Yes
	Double adjacent	4	27	28	96.4	Yes
	Double non-adjacent	4	23	43	53.5	No

[a] A "yes" in this column means that the actual number of correct choices made by the subjects was significantly greater than the number expected if the subjects were randomly choosing the correct box out of three (the probability of succeeding by doing this is 0.5), according to the binomial distribution (alpha = 0.05). Please refer to the Data Analysis section in Chapter 2 for more details.

I also calculated the percentages of the different types of errors and successes in adjacent and non-adjacent double invisible displacement trials (see Table 5). There was no significant difference between the percentage of second-choice errors in non-adjacent and adjacent trials (Wilcoxon signed ranks exact test: Total N = 4; ties = 0; ns). Post-hoc analysis showed that there was no significant difference between the percentage of first-choice errors in non-adjacent and adjacent trials (Wilcoxon signed ranks exact test: Total N = 4; ties = 1; ns).

Table 5. Mean Percentage of First- and Second-Choice Successes and Errors for Orangutans in Double Invisible Displacements in Phase II.

	First choice		Second choice	
Type of displacement	Success	Error	Success	Error
Adjacent	75.4	4.1	20.5	0
Non-adjacent	42.9	28.5	6.2	22.4

Discussion

Phase I

Orangutans as a group passed all regular tasks that required a single displacement (i.e., single, sequential, and alternate visible tasks, as well as single, sequential, and alternate invisible tasks). These results replicated those of previous researchers who studied apes (Barth & Call, 2006; Call, 2001; Collier-Baker et al., 2006; de Blois et al., 1998). However, as discussed previously, regular tasks can be solved by the use of the strategy "search in the box visited by the experimenter," and thus, control tasks (in which the empty displacer is moved into a second box, after the reward is left in the first box visited) need to be administered and analyzed, before firm conclusions can be drawn about the ability to solve single displacement tasks. Previous researchers have found that orangutans (de Blois et al., 1998) and chimpanzees (Collier-Baker et al., 2006) can solve single invisible displacement controls (these are the only single displacement controls that apes have been tested on). The present study used controls for all tasks, and found that orangutans passed most single displacement controls. A complete analysis showed that subjects were distinguishing between the two boxes visited by the experimenter (a complete analysis to check for this had never been done in previous studies).

The only control tasks that orangutans failed were the alternate visible and invisible controls. However, only a low number of these control trials could be administered to only two subjects. Since there were larger sample sizes (both in terms of the number of trials, and the number of subjects) for the other tasks, it seems reasonable to conclude that the group of orangutans under study passed single visible and invisible displacement controls without the use of the following strategies: "search in the last location visited" and "randomly choosing between the two boxes visited by the experimenter." However, subjects might still have been using the strategy of "search in the first location visited," and analysis of double visible displacements is required to eliminate possible use of this strategy.

Orangutans in the present study did pass the double visible displacement regular task. This finding replicates that of previous researchers who studied apes (Call, 2001; de Blois et al., 1998), and adds further confirmation because I conducted a complete analysis to ensure that the subjects were indeed distinguishing between the two boxes visited by the experimenter. Success on the double visible displacement regular task shows that subjects were not using the strategy of "search in the first location visited." Since subjects passed both the single visible controls, and the double visible displacement regular task, it can be concluded that they successfully passed visible displacement tasks without the use of any known strategy. Subjects in the present study also passed double visible displacement controls, which further strengthens this conclusion.

When the double visible displacement regular task was divided into adjacent and non-adjacent trials, subjects were found to solve adjacent, but not non-adjacent, trials.[7] Post-

[7] The only other study to divide this task in this manner was conducted by Call (2001), who found that chimpanzees and orangutans solved both types of trials.

hoc analysis showed that on the double visible non-adjacent trials, the number of choices to the irrelevant center box were significantly more than the number of choices to the visited but unbaited box. This indicates that the experimenter's "skipping of a box" (which does not arise in an adjacent trial), makes a non-adjacent trial more difficult, thus leading to a response of picking the center box (the same problem arose in the double invisible tasks as can be seen later in this discussion).

Orangutans as a group passed the double invisible displacement regular task in the present study.[8] This task was divided into adjacent and non-adjacent trials, and orangutans were found to solve adjacent, but not non-adjacent, trials. These findings replicate those of previous researchers who studied apes (Barth & Call, 2006; Call, 2001; Collier-Baker & Suddendorf, 2006; de Blois et al., 1998). However, my results differ from previous work when comparing the different types of successes and errors in adjacent and non-adjacent trials. In particular, previous researchers (Call, 2001; Collier-Baker & Suddendorf, 2006) found a significantly greater percentage of second-choice errors in non-adjacent trials, when compared to adjacent trials, which meant that after having chosen a relevant box, subjects were usually choosing the center box (which was never visited by the experimenter). This finding led Call (2001) to put forth the response-bias inhibition hypothesis, which states that apes have a bias towards searching in a sequence, with an inability to inhibit choosing the center box on non-adjacent trials. In contrast, my study did not fully replicate this previous finding-- although my subjects did make a greater percentage of second-choice errors in non-adjacent, when compared to

[8] Subjects failed controls trials in double invisible displacements.

adjacent trials, it could not be determined whether or not this difference was statistically significant, because of a low sample size.

However, a closer look at my results shows some support for the response-bias inhibition hypothesis, though in a different way. Whenever my subjects did get a second chance, after having chosen a relevant box on their first choice in non-adjacent trials, they always (100% of the time) chose the unbaited center box that was never visited by the experimenter. Another interesting finding was that my subjects made a greater percentage of *first-choice errors* in non-adjacent, compared to adjacent trials, although post-hoc analysis showed that this difference was not statistically significant (the role of first-choice errors has not been discussed in previous research). Thus, it appears that both first and second-choice errors contribute to the overall failure in the non-adjacent double invisible displacement trials (see Table 3).[9]

In sum, orangutans in the present study passed all visible and invisible displacement tasks, except for the non-adjacent trials in double visible and double invisible displacements. Since the possible use of all known strategies was eliminated with the analysis of the visible displacement tasks, it can be concluded that orangutans understand that an object continues to exist even when it is not perceived, and are capable of tracking successive visible displacements, but with some limitations in non-adjacent displacements. Since the use of the strategy of "randomly choosing between the two boxes visited by the experimenter" was not found in the visible and invisible

[9] This was the case in Call (2001) as well. His subjects made a larger number of first-choice errors in non-adjacent trials, as opposed to adjacent trials (although this difference was not significant). Along with his finding of a significantly greater number of second-choice errors in non-adjacent trials, this implies that both types of errors were contributing to his overall finding of a failure in non-adjacent double invisible displacements.

displacement control tasks, it would be reasonable to conclude that they are not using this strategy to solve adjacent trials in the double invisible displacement task. It can thus be concluded that orangutans are capable of representing the unperceived trajectory of an object, but with some limitations because they failed non-adjacent and control trials in double invisible displacements.

Phase II

As discussed in the introduction, Phase II was conducted to answer one of the questions that researchers of object permanence in primates are currently trying to answer. Are apes capable of representing the unperceived trajectory of an object, but with some limits to this capacity? Or are these performance limitations a result of the manner in which the tasks are presented? Call (2001) hypothesized that arranging the boxes close together in space might be causing the response bias of searching in a sequence, with an inability to inhibit choosing the center box. He suggested presenting tasks in a locomotive (not a small-scale) space, because having to move from one location to another might introduce costs associated with traveling and may reduce the tendency to search in locations that have not been visited by the experimenter (that is, the center box). If apes succeed on non-adjacent double invisible displacement trials in locomotive space, it would confirm that they are indeed fully capable of representing the unperceived trajectory of an object. Thus, one goal of this dissertation was to present double invisible displacement tasks to orangutans in a locomotive space, to see if they could solve non-adjacent double invisible displacement trials.[10]

[10] I also tried to administer the other tasks in the battery for comparative purposes; however, the number of trials per task that I was able to administer was too low for any reliable conclusions to be drawn.

Orangutans passed the double invisible displacement regular task in Phase II. As in Phase I, when this task was divided into adjacent and non-adjacent trials, orangutans were found to solve the former, but not the latter. The pattern of the different types of errors and successes in Phase II was very similar to that in Phase I. As in Phase I, it appeared that both first and second-choice errors contributed to the overall failure in the non-adjacent double invisible displacement trials. The percentage of second-choice errors was greater in non-adjacent, when compared to adjacent trials, although this difference was not statistically significant. Similarly, post-hoc analysis showed that the percentage of first-choice errors was greater in non-adjacent, when compared to adjacent trials, although this difference was not statistically significant. (see Table 5). Thus, presenting the boxes in locomotive space did not reduce the tendency to search in a location that was not visited by the experimenter. Further research is required to resolve the question of whether this performance limitation is a result of the manner in which the tasks are presented.

CHAPTER 4

GORILLAS: RESULTS AND DISCUSSION

Pretest

All the gorillas were able to unambiguously point with their fingers to their chosen box (if they could reach the box, they would even touch their chosen box with one or more fingers).

Phase I

Visible Displacement Tasks

Gorillas performed above chance on single, sequential, and alternate visible displacement *regular* tasks (binomial distribution, $p < 0.05$). Gorillas also performed above chance on single visible displacement *controls* (binomial distribution, $p < 0.05$). Further analysis showed that there was a significant difference between the number of choices to the baited box and the number of choices to the unbaited visited box on these controls (binomial distribution, $p < 0.05$). Control trials for sequential and alternate visible displacements could not be conducted because of a lack of subject motivation to participate.

Gorillas performed above chance on the double visible displacement regular task (binomial distribution, $p < 0.05$). However, further analysis showed that there was no significant difference between the number of choices to the baited box and the number of choices to the unbaited visited box on these displacements (binomial distribution, $p > 0.05$).

Double visible displacements were divided into adjacent and non-adjacent trials. Gorillas did not perform above chance on adjacent trials (binomial distribution, $p > 0.05$). Furthermore, post-hoc analysis indicates that for these trials, there was no significant difference between the number of choices to the baited box and the number of choices to the unbaited visited box (binomial distribution, $p > 0.05$). Gorillas performed above chance on non-adjacent trials (binomial distribution, $p < 0.05$). However, further analysis showed that there was no significant difference between the number of choices to the baited box and the number of choices to the unbaited visited box on non-adjacent trials (binomial distribution, $p > 0.05$).

Gorillas did not perform above chance on double visible controls (binomial distribution, $p > 0.05$).

Please refer to Table 6 for a summary of gorilla performance on visible displacement tasks in Phase I.

Table 6. Gorilla Performance on Visible Displacement Tasks in Phase I.

		No. of subjects	No. correct	Total no. of trials	Percent correct	Above chance?[a]	Distinguished between the two visited boxes?[b]	Passed task?[c]
Regular								
	Single	2	8	8	100	Yes	--	Yes
	Sequential	2	10	14	71.4	Yes	--	Yes
	Alternate	2	21	34	61.8	Yes	--	Yes
	Double	2	14	22	63.6	Yes	No	No
	Double adjacent	2	7	12	58.3	No	No[d]	No
	Double non-adjacent	2	7	10	70	Yes	No	No
Control								
	Single	2	7	8	87.5	Yes	Yes	Yes
	Double	2	7	12	58.3	No	--	No

Note. Dashes indicate that it was not necessary to check whether subjects were using the strategy of "randomly choosing between the two boxes visited by the experimenter," because it was not applicable (that is, for single, sequential, and alternate regular trials, and double visible controls).

Table 6 (continued)

[a] A "yes" in this column means that the actual number of correct choices made by the subjects was significantly greater than the number expected if the subjects were randomly choosing one box out of three (the probability of succeeding by doing this is 0.33), according to the binomial distribution (alpha = 0.05).

[b] A "yes" in this column means that the subjects were not using the strategy of "randomly choosing between the two boxes visited by the experimenter." The number of choices to the baited box was significantly greater than the number of choices to the non-baited visited box, according to the binomial distribution (alpha = 0.05).

[c] A "yes" in this column means that all possible strategies have been eliminated. This varies from task to task. A "no" means that subjects either did not perform above chance, or performed above chance, but did not distinguish between the two visited boxes. Please refer to the Data Analysis section in Chapter 2 for more details.

[d] Post-hoc analysis showed that subjects were not distinguishing between the two boxes visited by the experimenter in double visible adjacent trials.

Invisible Displacement Tasks

Gorillas performed above chance on single, sequential, and alternate invisible displacement *regular* tasks (binomial distribution, $p < 0.05$). Gorillas did not perform above chance on single invisible *controls* (binomial distribution, $p > 0.05$). Control trials for sequential and alternate invisible displacements could not be conducted because of a lack of subject motivation to participate.

Gorillas did not perform above chance on the double invisible displacement task (binomial distribution, $p > 0.05$). This task was divided into adjacent and non-adjacent trials. Gorillas performed above chance on adjacent (binomial distribution, $p < 0.05$), but not on non-adjacent (binomial distribution, $p > 0.05$) double invisible displacements. Gorillas did not perform above chance on double invisible controls (binomial distribution, $p > 0.05$).

Please refer to Table 7 for a summary of gorilla performance on invisible displacement tasks in Phase I.

I also calculated the percentages of the different types of errors and successes in adjacent and non-adjacent double invisible displacement trials (see Table 8). However, since there were only two gorillas, I did not run any statistical analyses on the data.

Table 7. Gorilla Performance on Invisible Displacement Tasks in Phase I.

		No. of subjects	No. correct	Total no. of trials	Percent correct	Above chance?[a]	Distinguished between the two visited boxes?[b]	Passed task?[c]
Regular								
	Single	2	7	9	77.8	Yes	--	Yes
	Sequential	2	10	15	66.7	Yes	--	Yes
	Alternate	2	14	28	50	Yes	--	Yes
	Double	2	19	36	52.8	No	--	No
	Double adjacent	2	13	17	76.5	Yes	--	Yes
	Double non-adjacent	2	6	19	31.6	No	--	No
Control								
	Single	2	5	11	45.5	No	--	No
	Double	2	4	12	33.3	No	--	No

Note. Dashes indicate that it was not necessary to check whether subjects were using the strategy of "randomly choosing between the two boxes visited by the experimenter," because it was either not applicable (that is, for single, sequential, alternate, and double regular trials, and double invisible controls), or because subjects did not perform above chance (for instance, single controls).

Table 7 (continued)

[a] A "yes" in this column means that the actual number of correct choices made by the subjects was significantly greater than the number expected if the subjects were randomly choosing one box out of three (the probability of succeeding by doing this is 0.33), according to the binomial distribution (alpha = 0.05). This applies for all tasks, except for double invisible displacements (including adjacent, non-adjacent, and control trials), in which case, probability of chance success is 0.5.

[b] A "yes" in this column means that the subjects were not using the strategy of "randomly choosing between the two boxes visited by the experimenter." The number of choices to the baited box was significantly greater than the number of choices to the non-baited visited box, according to the binomial distribution (alpha = 0.05).

[c] A "yes" in this column means that all possible strategies have been eliminated. This varies from task to task. A "no" means that subjects either did not perform above chance, or performed above chance, but did not distinguish between the two visited boxes. Please refer to the Data Analysis section in Chapter 2 for more details.

Table 8. Mean Percentage of First- and Second-Choice Successes and Errors for Gorillas in Double Invisible Displacements in Phase I.

	First choice		Second choice	
Type of displacement	Success	Error	Success	Error
Adjacent	60.7	10	17.2	12.2
Non-adjacent	27.9	63.7	0	8.3

Phase II

Only regular double invisible displacements were administered in this phase. Gorillas did not perform above chance on the double invisible displacement task (binomial distribution, $p > 0.05$). This task was divided into adjacent and non-adjacent trials. Gorillas performed above chance on adjacent (binomial distribution, $p < 0.05$), but not on non-adjacent (binomial distribution, $p > 0.05$) double invisible displacements. Please refer to Table 9 for a summary of gorilla performance in Phase II.

Table 9. Gorilla Performance on Double Invisible Displacements in Phase II.

		No. of subjects	No. correct	Total no. of trials	Percent correct	Above chance?[a]
Invisible						
	Double	2	29	48	60.4	No
	Double adjacent	2	19	19	100	Yes
	Double non-adjacent	2	10	29	34.5	No

[a] A "yes" in this column means that the actual number of correct choices made by the subjects was significantly greater than the number expected if the subjects were randomly choosing the correct box out of three (the probability of succeeding by doing this is 0.5), according to the binomial distribution (alpha = 0.05). Please refer to the Data Analysis section in Chapter 2 for more details.

I also calculated the percentages of the different types of errors and successes in adjacent and non-adjacent double invisible displacement trials (see Table 10). However, since there were only two gorillas, I did not run any statistical analyses on the data.

Table 10. Mean Percentage of First- and Second-Choice Successes and Errors for Gorillas in Double Invisible Displacements in Phase II.

	First choice		Second choice	
Type of displacement	Success	Error	Success	Error
Adjacent	83.9	0	16.1	0
Non-adjacent	34.9	25.7	0	39.4

Discussion

Phase I

Gorillas passed all regular tasks that required a single displacement (i.e., single, sequential, and alternate visible and invisible tasks). These results replicated those of previous researchers who studied apes (Barth & Call, 2006; Call, 2001; Collier-Baker et al., 2006; de Blois et al., 1998). However, as discussed previously, regular tasks can be solved by the use of the strategy "search in the box visited by the experimenter," and thus, control tasks (in which the empty displacer is moved into a second box, after the reward is left in the first box visited) need to be administered and analyzed. In the present study, I was able to administer controls for two single displacement tasks-- single visible and invisible.[11] A complete analysis showed that subjects could solve single visible, but not invisible, controls. The finding that subjects could not solve single invisible controls

[11] I was not able to conduct controls for sequential and alternate visible and invisible tasks because of a lack of subject motivation.

differs from that of previous research with other apes, which has found that orangutans (de Blois et al., 1998) and chimpanzees (Collier-Baker et al., 2006) can solve single invisible displacement controls (these are the only single displacement controls that apes have been tested on; gorillas have not been tested on single controls previously). This discrepancy could be a result of species differences, or could be an artifact of the low sample size in this study (I was able to test only two gorillas). Thus, more studies with suitable controls and complete analyses need to be conducted before any final conclusions can be drawn about this species' performance on single displacement tasks.

Gorillas in the present study failed the double visible displacement regular task because they were not distinguishing between the two boxes visited by the experimenter. When this task was divided into adjacent and non-adjacent trials, gorillas were found to fail both (and in non-adjacent trials, they were not distinguishing between the two boxes visited). Gorillas also failed double visible displacement controls. These findings differ from those of previous researchers who studied orangutans (Call, 2001; de Blois et al., 1998); however, these researchers did not check to see if their subjects were distinguishing between the two boxes visited in the regular trials (gorillas have not been tested on the double visible displacement task previously). The discrepancy could also be a result of species differences, or could be an artifact of the low sample size in this study. Thus, more studies with suitable controls and complete analyses need to be conducted before any final conclusions can be drawn about this species' performance on double visible displacement tasks.

Gorillas failed the double invisible displacement regular task in the present study.[12] This task was divided into adjacent and non-adjacent trials, and gorillas were found to solve adjacent, but not non-adjacent trials. These findings replicate those of previous researchers who studied apes (Barth & Call, 2006; Call, 2001; Collier-Baker & Suddendorf, 2006; de Blois et al., 1998). Gorillas did not make a greater percentage of *second-choice errors* in non-adjacent compared to adjacent trials (in fact, they made a slightly smaller percentage of errors). However, as with the orangutans in this study, whenever the gorillas did get a second chance on non-adjacent trials, they always (100% of the time) chose the unbaited center box that was never visited by the experimenter. Also, as with the orangutans, gorillas made a greater percentage of *first-choice errors* in non-adjacent trials (64%, as opposed to 10% on adjacent trials), although it could not be determined whether or not this difference was statistically significant, because of a low sample size. Thus, it appears that both first and second-choice errors contributed to the overall failure in the non-adjacent double invisible displacement trials for gorillas too (see Table 8).

Finally, I want to draw attention to the fact that gorillas in this study passed adjacent trials in double *invisible* displacement tasks, while failing adjacent double *visible* regular trials. This may seem surprising, given the assumption by previous researchers that double invisible displacement tasks are more difficult to solve than any other task. However, post-hoc analysis indicates that for the adjacent trials in the double *visible* task, subjects were not distinguishing between the two boxes visited by the experimenter, and for this task, subjects were given only one choice per trial. In the adjacent double *invisible* displacements, however, subjects were given two choices, and the fact that they

[12] Gorillas also failed double invisible displacement control trials.

passed these trials means that they were choosing among the two boxes visited by the experimenter. Thus, they might be succeeding in the adjacent double *invisible* displacement trials by using the strategy of "randomly choosing between the two visited boxes"; the fact that they were given two choices was an advantage. One can hypothesize that if subjects were given a second choice in the double visible task, they might have passed adjacent trials there as well.

Taken together, these results indicate that gorillas in this study could not solve visible and invisible displacement tasks in Phase I. However, given the low sample size, further research is required before any final conclusions can be drawn about the species' ability to represent unperceived objects and object movements.

Phase II

Gorillas failed the double invisible displacement regular task in Phase II. When this task was divided into adjacent and non-adjacent trials, gorillas were found to solve the former, but not the latter. As hypothesized in Phase I, subject could have passed the adjacent trials in Phase II simply because they were given two choices.

Gorillas made a greater percentage of *second-choice errors* in non-adjacent compared to adjacent trials (in fact, they did not make any second-choice errors in the adjacent trials). As in Phase I, whenever the gorillas were given a second chance in non-adjacent trials, they always (100% of the time) chose the unbaited center box that was never visited by the experimenter. Also, as in Phase I, gorillas made a greater percentage of *first-choice errors* in non-adjacent trials (in fact, they did not make any first-choice errors in the adjacent trials). Thus, it appears that both first and second-choice errors contributed to the overall failure in the non-adjacent double invisible displacement trials in Phase II

as well (see Table 10). As with the orangutans in this study, presenting the boxes in locomotive space for gorillas did not reduce the tendency to search in a location that was not visited by the experimenter. Further research is required to resolve the question of whether this performance limitation is a result of the manner in which the tasks are presented.

CHAPTER 5

BLACK-AND-WHITE RUFFED LEMURS: RESULTS AND DISCUSSION

Pretest

The lemurs had to be trained to point with their noses using a basic shaping procedure. On average, it took three 15 minute sessions to train each lemur to unambiguously point to one box out of an array of three (upon the prompt "where is it?"). "It" refers to the reward.

Phase I

Visible Displacement Tasks

Lemurs performed above chance on single, sequential, and alternate visible displacement *regular* tasks (binomial distribution, $p < 0.05$). Lemurs also performed above chance on sequential visible displacement *controls* (binomial distribution, $p < 0.05$). However, further analysis showed that there was no significant difference between the number of choices to the baited box and the number of choices to the unbaited visited box on sequential visible controls (binomial distribution, $p > 0.05$). Lemurs did not perform above chance on single and alternate visible displacement controls (binomial distribution, $p > 0.05$). Furthermore, post-hoc analysis showed that that there was no significant difference between the number of choices to the baited box

and the number of choices to the unbaited visited box on single and alternate visible controls (binomial distribution, $p > 0.05$).

Lemurs performed above chance on the double visible displacement *regular* task overall, and on both adjacent and non-adjacent trials (binomial distribution, $p < 0.05$), and further analysis showed that that there was a significant difference between the number of choices to the baited box and the number of choices to the unbaited visited box on all these displacements (binomial distribution, $p < 0.05$). Lemurs also performed above chance on double visible displacement *controls* (binomial distribution, $p < 0.05$).

Please refer to Table 11 for a summary of lemur performance on visible displacement tasks in Phase I.

Table 11. Black-and-White Ruffed Lemur Performance on Visible Displacement Tasks in Phase I.

		No. of subjects	No. correct	Total no. of trials	Percent correct	Above chance?[a]	Distinguished between the two visited boxes?[b]	Passed task?[c]
Regular								
	Single	5	23	30	76.7	Yes	--	Yes
	Sequential	5	26	32	81.3	Yes	--	Yes
	Alternate	5	51	62	82.3	Yes	--	Yes
	Double	5	31	44	70.5	Yes	Yes	Yes
	Double adjacent	5	16	22	72.7	Yes	Yes	Yes
	Double non-adjacent	5	15	22	68.2	Yes	Yes	Yes
Control								
	Single	5	10	20	50	No	No[d]	No
	Sequential	2	9	15	60	Yes	No	No
	Alternate	3	9	24	37.5	No	No[d]	No
	Double	5	17	34	50	Yes	--	Yes

Note. Dashes indicate that it was not necessary to check whether subjects were using the strategy of "randomly choosing between the two boxes visited by the experimenter," because it was not applicable (that is, for single, sequential, and alternate regular trials, and double visible controls).

Table 11 (continued)

[a] A "yes" in this column means that the actual number of correct choices made by the subjects was significantly greater than the number expected if the subjects were randomly choosing one box out of three (the probability of succeeding by doing this is 0.33), according to the binomial distribution (alpha = 0.05).

[b] A "yes" in this column means that the subjects were not using the strategy of "randomly choosing between the two boxes visited by the experimenter." The number of choices to the baited box was significantly greater than the number of choices to the non-baited visited box, according to the binomial distribution (alpha = 0.05).

[c] A "yes" in this column means that all possible strategies have been eliminated. This varies from task to task. A "no" means that subjects either did not perform above chance, or performed above chance, but did not distinguish between the two visited boxes. Please refer to the Data Analysis section in Chapter 2 for more details.

[d] Post-hoc analyses showed that subjects were not distinguishing between the two boxes visited by the experimenter in single and alternate controls.

Invisible Displacement Tasks

Lemurs performed above chance on single, sequential, and alternate invisible displacement *regular* tasks (binomial distribution, $p < 0.05$). Lemurs also performed above chance on single invisible displacement *controls* (binomial distribution, $p < 0.05$). Further analysis showed that there was a significant difference between the number of choices to the baited box and the number of choices to the unbaited visited box on single invisible controls (binomial distribution, $p < 0.05$). Lemurs did not perform above chance on alternate and sequential invisible displacement *controls* (binomial distribution, $p > 0.05$). Furthermore, post-hoc analysis showed that that there was no significant difference between the number of choices to the baited box and the number of choices to the unbaited visited box on alternate and sequential invisible controls (binomial distribution, $p > 0.05$).

Lemurs did not perform above chance on the double invisible displacement *regular* task (binomial distribution, $p > 0.05$). This task was divided into adjacent and non-adjacent trials. Lemurs performed above chance on adjacent (binomial distribution, $p < 0.05$), but not on non-adjacent (binomial distribution, $p > 0.05$) double invisible displacements. Lemurs did not perform above chance on double invisible *controls* (binomial distribution, $p > 0.05$).

Please refer to Table 12 for a summary of lemur performance on invisible displacement tasks in Phase I.

Table 12. Black-and-White Ruffed Lemur Performance on Invisible Displacement Tasks in Phase I.

		No. of subjects	No. correct	Total no. of trials	Percent correct	Above chance?[a]	Distinguished between the two visited boxes?[b]	Passed task?[c]
Regular								
	Single	5	20	26	76.9	Yes	--	Yes
	Sequential	5	27	31	87.1	Yes	--	Yes
	Alternate	5	41	51	80.4	Yes	--	Yes
	Double	5	23	39	58.9	No	--	No
	Double adjacent	5	15	20	75	Yes	--	Yes
	Double non-adjacent	5	8	19	42.1	No	--	No
Control								
	Single	5	19	27	70.4	Yes	Yes	Yes
	Sequential	2	4	8	50	No	No[d]	No
	Alternate	3	10	23	43.5	No	No[d]	No
	Double	5	3	20	15	No	--	No

Note. Dashes indicate that it was not necessary to check whether subjects were using the strategy of "randomly choosing between the two boxes visited by the experimenter," because it was not applicable (that is, for single, sequential, alternate, and double invisible regular trials, and double invisible controls).

[a] A "yes" in this column means that the actual number of correct choices made by the subjects was significantly greater than the number expected if the subjects were randomly choosing one box out of three (the probability of succeeding by doing this is 0.33), according to the binomial distribution (alpha = 0.05). This applies for all tasks, except for double invisible displacements, in which case, probability of chance success is 0.5.

Table 12 (continued)

[b] A "yes" in this column means that the subjects were not using the strategy of "randomly choosing between the two boxes visited by the experimenter." The number of choices to the baited box was significantly greater than the number of choices to the non-baited visited box, according to the binomial distribution (alpha = 0.05).

[c] A "yes" in this column means that all possible strategies have been eliminated. This varies from task to task. A "no" means that subjects either did not perform above chance, or performed above chance, but did not distinguish between the two visited boxes. Please refer to the Data Analysis section in Chapter 2 for more details.

[d] Post-hoc analyses showed that subjects were not distinguishing between the two boxes visited by the experimenter in sequential and alternate controls.

I also calculated the percentages of the different types of errors and successes in adjacent and non-adjacent double invisible displacement trials (see Table 13). The sample size was too low to run a Wilcoxon signed ranks exact test to compare the percentage of second-choice errors in adjacent and non-adjacent trials. Post-hoc analysis showed that there was no significant difference between the percentage of first-choice errors in non-adjacent and adjacent trials (Wilcoxon signed ranks exact test: Total N = 5; ties = 2; ns).

Table 13. Mean Percentage of First- and Second-Choice Successes and Errors for Black-and-White Ruffed Lemurs in Double Invisible Displacements in Phase I.

	First choice		Second choice	
Type of displacement	Success	Error	Success	Error
Adjacent	59.3	14	18.7	8
Non-adjacent	47.3	45.3	0	7.3

Discussion

Black-and-white ruffed lemurs as a group passed all regular tasks that required a single displacement (i.e., single, sequential, and alternate visible tasks, as well as single, sequential, and alternate invisible tasks). Recent research has found that other lemur species (red-fronted brown lemurs, mongoose lemurs, ring-tailed lemurs, and gentle bamboo lemurs) passed single *visible* regular tasks, but failed single *invisible* regular tasks (Deppe, Wright, & Szelistowski, 2009; it should be noted that all these species were combined into a single group during data analysis). However, as discussed previously, regular tasks can be solved by the use of the strategy "search in the box visited by the experimenter," and thus, control tasks need to be administered. My study found that

except for the single invisible displacement control task, lemurs failed all other controls for single displacements (i.e., single, sequential, and alternate visible controls, and sequential and alternate invisible controls). The failure was because the subjects were not distinguishing between the two boxes visited by the experimenter.

Black-and-white ruffed lemurs passed double visible displacement regular and control trials.[13] However, there was some imbalance in the double visible *controls* that I administered, in that the center box happened to be the baited box in a much larger number of trials than the terminal boxes. This was because the box to be baited was randomly pre-determined, and if subjects stopped participating after sometime, they might not have received all the trials in which the terminal boxes were supposed to be baited. A closer look at performance on double visible controls reveals that subjects performed very well on trials in which the center box was baited (subjects passed 14 out of 18 trials), but did not do so well on trials in which terminal boxes were baited (subjects passed only 3 out of 16 trials), which shows some limitations in their understanding of this task. Along with the finding that subjects failed most controls for single displacements, this casts some doubt on whether black-and-white ruffed lemurs in this study truly understood visible displacements.

Deppe et al. (2009) found that the various species of lemurs in their study succeeded on double visible displacement regular and control trials. However, they did not check to see if their subjects were distinguishing between the two boxes visited by the experimenter in the regular trials. Thus, we cannot rule out the possibility that subjects in

[13] When the double visible displacement regular task was divided into adjacent and non-adjacent trials, lemurs were found to pass both.

their study were using the strategy of "randomly choose between the two boxes visited" to solve double visible regular trials.

Lemurs as a group failed the double invisible displacement regular task in the present study,[14] as in Deppe et al. (2009). When this task was divided into adjacent and non-adjacent trials, lemurs were found to solve the former, but not the latter. Since subjects were not distinguishing between the two boxes visited by the experimenter in single displacement controls, they might be passing adjacent trials in double invisible displacements by using the strategy of "randomly choosing between the two visited boxes"; the fact that they were given two choices was an advantage. One can hypothesize that if subjects were given a second choice in the single displacement controls, they might have passed those as well.

In the double invisible displacement task, lemurs did not make a greater percentage of *second-choice errors* in non-adjacent compared to adjacent trials (in fact, they made a slightly smaller percentage of errors). However, as with the orangutans and gorillas in this study, whenever the lemurs did get a second chance on non-adjacent trials, they always (100% of the time) chose the unbaited center box that was never visited by the experimenter. Also, as with the orangutans and gorillas in this study, lemurs made a greater percentage of *first-choice errors* in non-adjacent trials, when compared to adjacent trials, although post-hoc analysis showed that this difference was not statistically significant. Thus, it appears that both first and second-choice errors contributed to the overall failure in the non-adjacent double invisible displacement trials for lemurs too (see Table 13).

[14] Lemurs also failed double invisible displacement control trials.

Taken together, these results indicate that black-and-white ruffed lemurs cannot solve tasks in the test battery of Phase I. Subjects could not be tested in Phase II because their enclosures were not suited for the method used.

CHAPTER 6

GENERAL DISCUSSION

Phase I

One of the goals of this dissertation was to test different primate species on all tasks in the traditional object permanence test battery, using controls for every task in the battery. A literature review reveals that very few studies of object permanence in non-human primates have been conducted using appropriate controls. The present study was the first to conduct control trials for all tasks in the battery, and is thus a more thorough evaluation of object permanence in the species under study.

Another goal of this dissertation was to try and ensure that no simple search strategies could account for success in solving the tasks in the traditional test battery. Some previous studies have controlled for strategies such as "search in the last box visited by the experimenter" and "search in the first box visited by the experimenter." While the present study also controlled for these strategies, I found that subjects could appear to succeed[15] on some tasks in which there are two displacements (i.e., single, sequential, and alternate visible and invisible controls, as well as double visible regular trials) by using the strategy of "randomly choosing between the two boxes visited by the experimenter." Whether they are using this strategy or not can be revealed by comparing the number of choices to the baited box with the number of choices to the non-baited visited box. If there is no significant difference, then it can be concluded that subjects have failed the task because they are not distinguishing between the two boxes visited by the

[15] Success is defined as "performing above chance," which means that the actual number of correct choices made by the subjects was significantly greater than the number expected if the subjects were randomly choosing one box out of three (the probability of succeeding by doing this is 0.33).

experimenter. Incidentally, if subjects are not performing above chance on the aforementioned tasks, post-hoc analyses might reveal that the reason for failure was that they were not distinguishing between the two boxes visited by the experimenter.

Having administered all tasks with suitable controls, I found that orangutans were the only species that reliably passed most visible and invisible displacement tasks in the traditional object permanence test battery. Since the possible use of all known strategies was eliminated with the analysis of the visible displacement tasks, it can be concluded that orangutans understand that an object continues to exist even when it is not perceived, and are capable of tracking successive visible displacements, but with some limitations in non-adjacent displacements. It can thus be concluded that orangutans are capable of representing the unperceived trajectory of an object, but with some limitations because they failed non-adjacent and control trials in double invisible displacements. These findings are similar to those from previous object permanence research with orangutans (Barth & Call, 2006; Call 2001; de Blois et al., 1998), and add further confirmation to previous conclusions on object permanence in orangutans, because I conducted a complete analysis to ensure that the subjects were indeed distinguishing between the two boxes visited by the experimenter in tasks requiring two displacements.

In contrast, the possible use of all known strategies could not be eliminated when analyzing the data on gorillas and black-and-white ruffed lemurs in the present study. Both species failed some tasks because they were not distinguishing between the two boxes visited by the experimenter (gorillas failed the double visible task, and lemurs failed most single displacement controls in this way), and thus, both species' apparent success on the adjacent trials in double invisible displacements was called into question.

Both species also failed non-adjacent and control trials in double invisible displacements. While more studies need to be conducted with gorillas (since this study could only test two individuals), it can be concluded that black-and-white ruffed lemurs lack the ability to represent unperceived objects and object movements. Furthermore, the finding that subjects used the strategy of "randomly choosing between the two boxes visited" in some tasks warrants a re-evaluation of object permanence in all species studied to date. Future studies of object permanence should test for this strategy as well.

Finally, it appeared that both first and second-choice errors[16] contributed to the overall failure in the non-adjacent double invisible displacement trials for all three species in the present study. The presence of both of these errors is indicative of the inherent difficulty of non-adjacent trials. The presence of second-choice errors, specifically, lends support to Call's (2001) response-bias inhibition hypothesis, which states that primates have a bias towards searching in a sequence, with an inability to inhibit choosing the center box in non-adjacent trials. In particular, whenever my subjects received a second chance, after having chosen a relevant box on their first choice, they always (100% of the time) chose the unbaited center box that was never visited by the experimenter. This was the case for all species under study.

In sum, results from this dissertation indicate that orangutans were the only species under study with an ability to represent unperceived objects and an ability to represent unperceived object movements. This is surprising, given the previously stated hypotheses that the former ability might have evolved in species that forage for plant food that

[16] First-choice errors occur if a subject chooses a non-baited, non-visited box on the first attempt. Second-choice errors occur if a subject chooses the visited, non-baited box on the first attempt, and the non-visited box on the second attempt.

remains at a certain location even when it is not perceived, and the latter ability might have evolved in species that need to track group members. Orangutans, gorillas, and black-and-white ruffed lemurs forage for this kind of plant food, and all three species live in social groups. Thus, the finding that orangutans were the only species with an ability to represent unperceived objects and object movements calls these hypotheses into question. Taking a closer look at each species' ecology (Table 14) might give us a better understanding of these findings.

Table 14. Brief ecological comparison of Sumatran orangutans, Western lowland gorillas, and black-and-white ruffed lemurs.

	Sumatran orangutans	**Western lowland gorillas**	**Black-and-white ruffed lemurs**
Foraging for stationary plant foods that remain at a given location even when they are not perceived	Yes (MacKinnon, 1974; Maple, 1980)	Yes (Doran et al., 2002; Maple, 1982)	Yes (Vasey, 2003)
Extractive foraging	Yes, to some extent (Gibson, 1986; Parker & Gibson, 1979; van Schaik, Fox, & Sitompul 1996)	Minimal (extract pith, tubers) (Gibson, 1986; Parker & Gibson, 1979; Tomasello & Call, 1997)	None reported
Living in social groups and having to keep track of moving group members	Yes, to some extent (Cawthon Lang, 2005)	Yes (Doran & McNeilage, 2001)	Yes (Vasey, 2003)
Needing to keep track of mobile predators	Yes, to some extent (Cawthon Lang, 2005)	Possibly leopards (Fay et al., 1995)	Yes (Vasey, 2003)
Consuming mobile prey (eg: ants, termites)	Minor component of diet (MacKinnon, 1974; Maple, 1980)	Minor component of diet (Doran et al., 2002; Maple, 1982)	No (Vasey, 2003)

As discussed previously, it has been hypothesized that the ability to represent unperceived objects might have evolved within the context of foraging, including extractive foraging (Tomasello & Call, 1997). As can be seen from Table 14, all three species under study forage for plant foods that remain at a given location. However, out of the three species, only orangutans and gorillas can be considered to be extractive foragers. Specifically, orangutans extract pith and tubers (Gibson, 1986; Parker & Gibson, 1979) and have been observed to use sticks to extract seeds out of fruit husks and probe for insects in the wild (van Schaik et al., 1996). Gorillas also extract pith and tubers in the wild (Doran et al., 2002; Gibson, 1986; Parker & Gibson, 1979), although to a lesser degree. In contrast, black-and-white ruffed lemurs are not considered to be extractive foragers. Since extractive foraging requires extracting a food that is not directly perceptible, it has been hypothesized that extractive foragers might have evolved the ability to mentally represent unperceived objects (Tomasello & Call, 1997). Given the finding of this study that orangutans (and not black-and-white ruffed lemurs) have the ability to represent unperceived objects, I believe that it is extractive foraging (and not general foraging) that is the major factor in the evolution of this ability.

I believe that the finding that the gorillas in this study could not represent unperceived objects, is an artifact of the low sample size (both in terms of the number of subjects, and the number of trials per task), and that further research with a larger sample size will yield more positive results. This might be possible even though gorillas do not extensively engage in extractive foraging in the wild, because it has been hypothesized that humans and great apes had a common omnivorous, tool-using ancestor, who engaged

in extractive foraging, and gorillas later radiated into a niche that did not require the use of tools and a high degree of extractive foraging (Gibson, 1986; Parker & Gibson, 1979).

Since this study found that black-and-white ruffed lemurs cannot represent unperceived objects, it is not expected that they can represent unperceived object movements. Thus, the following discussion will focus on possible reasons for why orangutans are able to represent unperceived object movements, and reasons for why we might expect gorillas to have the same ability. It has been hypothesized that this ability might have evolved in species that need to track mobile prey, predators, or group members (Tomasello & Call, 1997). As can be seen from Table 14, both gorillas and orangutans live in groups: western lowland gorillas live in groups of 10-20 individuals in the wild (Doran & McNeilage, 2001), whereas orangutans in the wild interact socially during breeding and when taking care of offspring (MacKinnon, 1974; Maple, 1980). Orangutans are subject to occasional predation by tigers (Cawthon Lang, 2005), and leopards are possible predators of gorillas (Fay, Carroll, Kerbis Peterhans, & Harris, 1995). Both species also feed on mobile prey, specifically termites and ants, although these do not comprise a major portion of their diet (MacKinnon, 1974; Maple, 1980, 1982; Doran et al., 2002).

Since neither species seems to be under strong predation pressure, and neither species consumes a large amount of mobile prey, it would be reasonable to accept Tomasello and Call's (1997) hypothesis that apes' ability to represent unperceived object movements might have evolved mainly in the context of tracking group members. As before, I believe that the finding that gorillas in this study could not represent unperceived object movements is an artifact of the low sample size. A question might arise about why this

ability did not evolve in black-and-white ruffed lemurs, which also live in groups. However, it must be noted that a particular demand might not necessarily lead to the same outcome in different animal taxa, especially if there is not a high degree of phylogenetic relatedness.

Phase II

In Phase II, tasks were presented to gorillas and orangutans in a locomotive space, to see if they could solve non-adjacent double invisible displacement trials (this is the first study to present these tests in a locomotive space to non-human primate species). Call (2001) hypothesized that arranging the boxes close together in space, as in the traditional test battery, might be causing the response bias of searching in a sequence, with an inability to inhibit choosing the center box. He suggested presenting tasks in a locomotive (not a small-scale) space, because having to move from one location to another might introduce costs associated with traveling and may reduce the tendency to search in locations that have not been visited by the experimenter (that is, the center box).

However, orangutans and gorillas in this study did not pass non-adjacent trials, even when tasks were presented in locomotive space. The pattern of the different types of errors and successes in Phase II was very similar to that in Phase I. As in Phase I, it appeared that both first and second-choice errors contributed to the overall failure in the non-adjacent double invisible displacement trials. Thus, presenting the boxes in locomotive space did not reduce the tendency to search in a location that was not visited by the experimenter. This is the first study to present this task to non-human primate species in locomotive space. Further research is required to resolve the question of

whether this performance limitation is a result of the manner in which the tasks were presented.

Apart from suggesting task presentation in locomotive space, Call (2001) also suggested that a *non-linear* arrangement of the boxes might remove apes' tendency to search in a sequence, with an inability to inhibit choosing the center box. To my knowledge, the only researchers to have implemented this methodological change are Collier-Baker and Suddendorf (2006). In a study of double invisible displacements, these researchers presented four boxes in a non-linear diamond-shaped array on a vertical plane to two chimpanzees (see Figure 4). The diamond-shaped array prevented the subjects from simply searching in a sequence, because the boxes were no longer in a row. The boxes were presented on a vertical plane so that all boxes were within reach of the subjects (and all boxes were equidistant to the subjects). They claimed that the chimpanzees successfully solved non-adjacent double invisible displacements (along with suitable control trials), and concluded that poor performance in previous studies might have been because of a search bias or inhibition problem caused by a linear array, and not because of the species' inability to solve this task. However, the displacements were not truly non-adjacent because they did not involve the experimenter skipping a box, as in the traditional linear arrangement, and thus their conclusion is invalid (their adjacent displacement consisted of, for example, visiting boxes A and B in sequence; their non-adjacent displacement consisted of visiting boxes D and B in sequence, the movement being straight across the diagonal from D to B, and not over A).

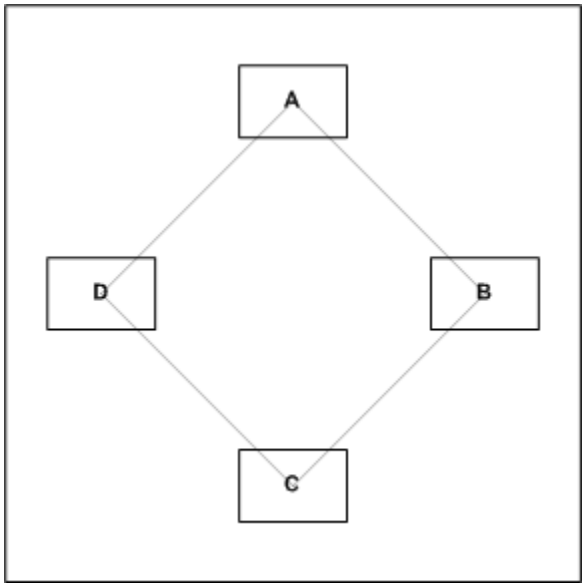

Figure 4. Depiction of diamond-shaped array.

I believe that a non-linear arrangement in which the experimenter *skips* a box is required to resolve the question of whether apes can truly solve non-adjacent displacements. I suggest presenting three boxes in a triangle-shaped array on a vertical plane (see Figure 5). The triangle should be equilateral so that the three boxes are equidistant from one another. An example of a non-adjacent displacement would be to move the displacer into box C, bring it out, move it over box A, and then moving it into box B (the reward could be hidden in either C or B). Using three boxes in this manner will yield results that can be directly compared with results from non-adjacent displacements in the traditional linear array (with three boxes in a row). With a triangle-shaped array, there will be no question of the subjects simply searching in a sequence, because the boxes are no longer in a row.

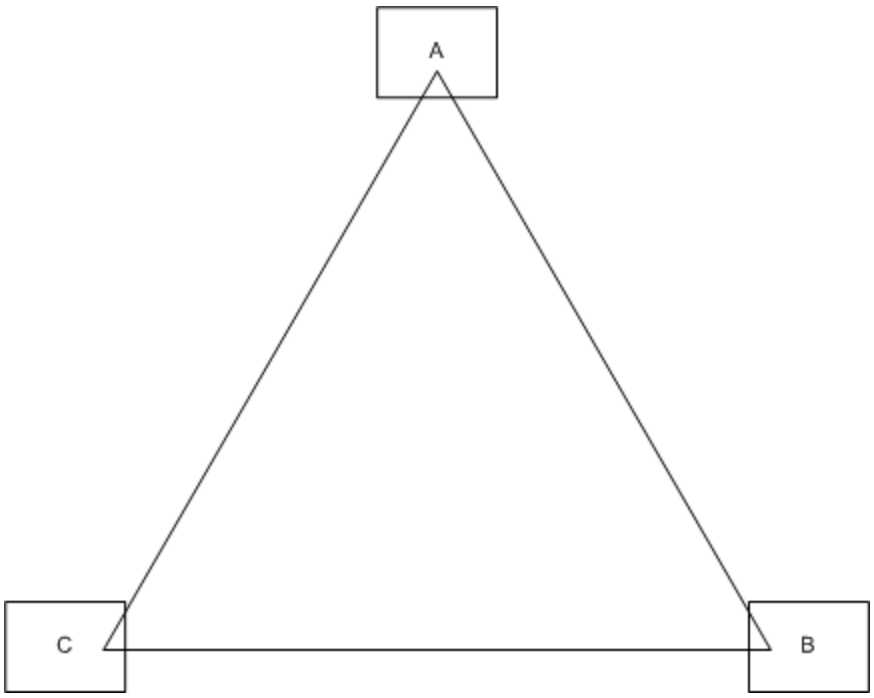

Figure 5. Depiction of triangle-shaped array.

Future Directions with the Traditional Paradigm

As has been repeatedly pointed out throughout this dissertation, there has been no uniformity in tasks that have been used to study object permanence in non-human primates. Not all studies have used all the tasks in the test battery, not all studies have used appropriate controls, and not all studies have used controls for each and every task in the battery. All of this inconsistency makes it very difficult to make valid species comparisons, or even to make valid within-species assessments. Furthermore, not all researchers will be able to use the sheer number of tasks in the battery for various reasons, including a lack of subject motivation to participate in so many tasks. For species that have never been subject to object permanence studies, control tasks in the battery (single, sequential, alternate visible and invisible) can first be administered to

check whether they understand that objects continue to exist even when they are not perceived. If species have demonstrated this understanding, I suggest that the following two tasks are adequate to test for an ability to track a visibly moving object and an ability to represent the unperceived trajectory of an object:

1. Double visible displacement. After the reward is placed in a transparent displacer, the displacer is successively moved into two of the three boxes, and the reward is left in one of the two visited boxes. The two boxes visited, the order in which they are visited, the initial and final positions of the displacer, and whether the reward is left in the first or second box visited, should all be randomized.

The analysis of the task should include a check to see if the subjects are distinguishing between the two boxes visited by the experimenter. This task, with the complete analysis, will thus control for all the three known strategies,[17] and so a separate control task is not required. Thus, it is a decisive test for visible displacements. Adjacent and non-adjacent trials can then be separately analyzed to see if there is any difference in the pattern of choices. In fact, adjacent and non-adjacent trials should be administered in separate blocks, one after the other. This is because if subjects have difficulty with non-adjacent trials, as has been found in the present study, interspersing them with adjacent trials might disrupt performance on the latter.

2. Double invisible displacement. This is similar to the task described above, except that an opaque displacer is used instead of a transparent displacer, and a second choice is given if the subject first chooses the unbaited visited box. This task will control for the strategies of "search in the first box visited by the experimenter" and "search in the last

[17] The three known strategies are: "search in the first box visited by the experimenter," "search in the last box visited by the experimenter," and "randomly choose between the two boxes visited by the experimenter."

box visited by the experimenter." However, we cannot truly conclude that subjects passed the double invisible displacement task, unless the same subjects also passed the double *visible* displacement task without the use of the three known strategies. Adjacent and non-adjacent trials can be administered in separate blocks.

Success on the double visible displacement task can be taken as evidence of an understanding that an object exists even when it is not perceived, and as evidence of an ability to track a visibly moving object. Success on both the visible and the invisible displacement tasks can be taken as evidence of an ability to represent the unperceived trajectory of an object.

Another line of research that is worth pursuing is whether individuals can *learn* to solve these tasks after training, if they fail during initial experiments. Previous researchers of object permanence have not looked at whether individuals can learn to solve tasks after training; in fact, they used a low number of trials to avoid the possibility of learning during the experiments. However, I believe that if subjects can solve visible and invisible tasks after training, it can be taken as evidence of object permanence. These training sessions can be conducted using a computerized testing system with a touch screen and an automated feeder for delivering reinforcers for correct responses. Such a system would eliminate auditory and visual cues that are inherent in traditional object permanence tasks, give the researcher an easy way to administer a large number of trials over a relatively short span of time, and allow a greater degree of flexibility in designing suitable experiments for different species.

REFERENCES

Aguiar, A., & Baillargeon, R. (2002). Developments in young infants' reasoning about occluded objects. *Cognitive Psychology, 45*(2), 267-336.

Antinucci, F., Spinozzi, G., Visalberghi, E., & Volterra, V. (1982). Cognitive development in a Japanese macaque (*Macaca fuscata*). *Annali dell'Istituto Superiore di Sanita, 18*, 177-184.

Baillargeon, R. (2008). Innate ideas revisited for a principle of persistence in infants' physical reasoning. *Perspectives on Psychological Science, 3*(1), 2-12.

Baillargeon, R. (1987). Object permanence in 3 $^{1}/_{2}$- and 4 $^{1}/_{2}$- month-old infants. *Developmental Psychology, 23*(5), 655-664.

Baillargeon, R. (1993). The object concept revisited: New directions in the investigation of infants' physical knowledge. In C. E. Ganrud (Ed.), *Carnegie-Mellon symposia on cognition: Vol. 23. Visual perception and cognition in infancy* (pp. 265-315). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.

Baillargeon, R. & Graber, M. (1987). Where is the rabbit? 5.5-month-old infants' representation of the height of a hidden object. *Cognitive Development, 2*, 375-392.

Baillargeon R, Spelke ES, Wasserman S. 1985. Object permanence in five-month-old infants. *Cognition, 20*, 191-208.

Baker, A. J., Bales, K., & Dietz, J. M. (2002). Mating system and group dynamics in lion tamarins. In. D. G. Kleiman & A. B. Rylands (Eds.), *Lion tamarins: biology and conservation* (pp. 188-212). Washington DC: Smithsonian Institution Press.

Barth, J., & Call, J. (2006). Tracking the displacement of objects: A series of tasks with great apes (*Pan troglodytes, Pan paniscus, Gorilla gorilla, and Pongo pygmaeus*) and young children (*Homo sapiens*). *Journal of Experimental Psychology: Animal Behavior Processes, 32*(3), 239-252.

Bogartz, R. S., & Shinskey, J. L. (1998). On perception of a partially occluded object in 6-month-olds. *Cognitive Development, 13*, 141-163.

Bogartz, R. S., Shinskey, J. L., & Speaker, C. (1997). Interpreting infant looking: The event set x event set design. *Developmental Psychology, 33*, 408-422.

Bremner, G. J., Johnson, S. P., Slater, A., Mason, U., Foster, K., Cheshire, A., & Spring, J. (2005). Conditions for young infants' perception of object trajectories. *Child Development, 76*(5), 1029-1043.

Byrne RW. (1994). The evolution of intelligence. In P. J. B. Slater & T. R. Halliday (Eds.), *Behavior and Evolution* (pp. 223-265). Cambridge: Cambridge University Press.

Call, J. (2000). Representing space and objects in monkeys and apes. *Cognitive Science, 24*(3), 397-422.

Call, J. (2001). Object permanence in orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*), and children (*Homo sapiens*). *Journal of Comparative Psychology, 115*, 159-171.

Cawthon Lang, K. A. (2005). *Primate factsheets: Orangutan (Pongo) taxonomy, morphology, & ecology.* Retrieved May 1, 2009, from Primate Info Net, Library and Information Service, National Primate Research Center, University of Wisconsin-Madison Website: http://pin.primate.wisc.edu/factsheets/entry/orangutan

Clutton-Brock, T. H., & Harvey, P. H. (1980). Primates, brains and ecology. *Journal of Zoology, 190,* 309-323.

Collier-Baker, E., Davis, J. M., Nielsen, M., & Suddendorf, T. (2006). Do chimpanzees (*Pan troglodytes*) understand single invisible displacement? *Animal Cognition, 9*, 55-61.

Collier-Baker, E., Davis, J. M., & Suddendorf, T. (2004). Do dogs (*Canis familiaris*) understand invisible displacement? *Journal of Comparative Psychology, 118*(4), 421-433.

Collier-Baker, E., & Suddendorf, T. (2006). Do chimpanzees (*Pan troglodytes*) and 2-year-old children (*Homo sapiens*) understand double invisible displacement? *Journal of Comparative Psychology, 120*(2), 89-97.

Cohen, L. B., Chaput, H. H., Cashon, C. H. (2002). A constructivist model of infant cognition. *Cognitive Development, 17*, 1323-1343.

de Blois S. T., & Novak M. A. (1994). Object permanence in rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology, 108*, 318-327.

de Blois S. T., Novak, M. A., Bond, M. (1998). Object permanence in orangutans (*Pongo pygmaeus*) and squirrel monkeys (*Saimiri sciureus*). *Journal of Comparative Psychology, 112*, 137-152.

de Blois, S. T., Novak, M. A., & Bond, M. (1999). Can memory requirements account for species' differences in invisible displacement tasks? *Journal of Experimental Psychology, 25*(2), 168-176.

Deppe, A. M., Wright, P. C., & Szelistowski, W. A. (2009). Object permanence in lemurs. *Animal Cognition, 12*(2), 381-388.

Doran, D. M., & McNeilage, A. (2001). Subspecific variation in gorilla behavior: The influence of ecological and social factors. In M. M. Robbins, P. Sicotte, & K. J. Stewart (Eds.), *Mountain gorillas: Three decades of research at Karisoke* (pp. 123-149). Cambridge: Cambridge University Press.

Doran, D. M., McNeilage, A., Greer, S., Bocian, C., Mehlman, P., & Shah, N. (2002). Western lowland gorilla diet and resource availability: New evidence, cross-site comparisons, and reflections on indirect sampling methods. *American Journal of Primatology, 58*, 91-116.

Doré, F. Y. (1986). Object permanence in adult cats (*Felis catus*). *Journal of Comparative Psychology, 100*, 340-347.

Doré F. Y. (1990). Search behavior in cats (*Felis catus*) in an invisible displacement test: cognition and experience. *Canadian Journal of Psychology, 44*, 359-370.

Dumas C. (1992). Object permanence in cats (*Felis catus*): an ecological approach to the study of invisible displacements. *Journal of Comparative Psychology, 106*, 404-410.

Dumas C., & Brunet, C. (1994). Object permanence in capuchin monkeys (*Cebus apella*): A study of invisible displacements. *Canadian Journal of Experimental Psychology, 48*, 341-357.

Dumas C., & Doré, F. Y. (1989). Cognitive development in kittens (*Felis catus*): A cross-sectional study of object permanence. *Journal of Comparative Psychology, 103*, 191-200.

Dumas C., & Doré, F. Y. (1991). Cognitive development in kittens (*Felis catus*): An observational study of object permanence and sensorimotor intelligence. *Journal of Comparative Psychology, 105*, 357-365

Dumas C., & Wilkie, D. W. (1995). Object permanence in ring doves (*Streptopelia risoria*). *Journal of Comparative Psychology, 2*, 142-150.

Dunbar, R. I. M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evolution, 20*, 469-493.

Dunbar, R. I. M. (1995). Neocortex size and group size in primates: a test of the hypothesis. *Journal of Human Evolution, 28*, 287-296.

Fay, J. M., Carroll, R., Kerbis Peterhans, J. C., & Harris, D. (1995). Leopard attack on and consumption of gorillas in the Central African Republic. *Journal of Human Evolution 29*(1), 93-99.

Fedor, A., Skollar, G., Szerencsy, N., & Ujhelyi, M. (2008). Object permanence tests on gibbons (*Hylobatidae*). *Journal of Comparative Psychology, 122*(4), 403-417.

Fiset, S., & LeBlanc, V. (2007). Invisible displacement understanding in domestic dogs (*Canis familiaris*): the role of visual cues in search behavior.

Funk, M. S. (1996). Development of object permanence in the New Zealand parakeet (*Cyanoramphus auriceps*). *Animal Learning and Behavior, 24*, 375-383.

Gagne, R. M. (1970). *The conditions of learning*. New York: Holt, Rinehart and Winston.

Gagnon S., & Doré, F. Y. (1992). Search behavior in various breeds of adult dogs (*Canis familiaris*): Object permanence and olfactory cues. *Journal of Comparative Psychology, 106*, 58-68.

Gagnon S., & Doré, F. Y. (1993). Search behavior of dogs (*Canis familiaris*) in invisible displacement problems. *Animal Learning and Behavior, 21*, 246-254.

Gagnon S., & Doré, F. Y. (1994). A cross-sectional study of object permanence in domestic puppies (*Canis familiaris*). *Journal of Comparative Psychology, 108*, 220-232.

Gelman, R. & Baillargeon, R. (1983). A review of some Piagetian concepts. In P. Mussen (Ed.), *Carmichael's manual of child psychology* (pp. 167-230). New York: Wiley.

Gibson, K. R. (1986). Cognition, brain size and the extraction of embedded food resources. In J. G. Else & P. C. Lee (Eds.), *Primate ontogeny, cognition, and social behavior* (pp. 93-103). Cambridge: Cambridge University Press.

Gomez, J. C. (2004). *Apes, monkeys, children, and the growth of mind*. Cambridge, MA: Harvard University Press.

Goodman, S. M. (2003). Mammals: predation on lemurs. In S. M. Goodman & J. P. Benstead (Eds.), *The natural history of Madagascar*, (pp. 1221-1228). Chicago: University of Chicago Press.

Goulet S., Doré, F. Y., & Rousseau, R. (1994). Object permanence and working memory in cats (*Felis catus*). *Journal of Experimental Psychology: Animal Behavior Processes, 20*, 347-365.

Gratch G. (1977). Review of Piagetian infancy research: Object concept development. In: W. E. Overton & J. M. Gallagher (Eds.), *Knowledge and development* (pp. 59-88). New York: Plenum Press.

Haith, M. M. (1988). Who put the cognition in infant cognition? Is rich interpretation too costly? *Infant Behavior and Development, 21*, 167-179.

Harris PL. 1975. Development of search and object permanence during infancy. *Psychological Bulletin, 82*, 332-344.

Kellman, P. J., & Spelke, E. S. (1983). Perception of partly occluded objects in infancy. *Cognitive Psychology, 15*, 483-524.

Kinzey, W. G. (1997). *New World Primates: Ecology, Evolution, and Behavior*. New York: Aldine de Gruyter.

Krojgaard, P. (2005). Infants' search for hidden persons. *International Journal of Behavioral Development, 29*(1), 70-79.

Luo, Y., Baillargeon, R., Brueckner, L., & Munakata, Y. (2003). Reasoning about a hidden object after a delay: Evidence for robust representations in 5-month-old infants. *Cognition, 88*(3), B23-B32.

MacKinnon, J. (1974). The behaviour and ecology of wild orang-utans (*Pongo pygmaeus). Animal Behaviour, 22*, 3-74.

Maple (1980). *Orang-utan Behavior*. New York: Van Nostrand Reinhold Company.

Maple (1982). *Gorilla Behavior*. New York: Van Nostrand Reinhold Company.

Mareschal, D., Johnson, M. H., Sirois, S., Spratling, M. W., Thomas, M. C., & Westermann, G. (2007). *Neuroconstructivism: Vol. 1- How the brain constructs*

Mathieu, M., & Bergeron, G. (1981). Piagetian assessment of cognitive development in chimpanzee (*Pan troglodytes*). In A. B. Chiarelli & R. S. Corruccini (Eds.), *Primate behavior and sociobiology* (pp. 142-147). New York: Springer.

Mathieu, M., Bouchard, M. A., Granger, L., & Herscovitch, J. (1976). Piagetian object permanence in *Cebus capucinus, Lagothrica flavicauda,* and *Pan troglodytes*. *Animal Behaviour, 24*, 585-588.

Meltzoff, A. N., & Moore, K. M. (1998). Object representation, identity, and the paradox of early permanence: Steps toward a new framework. *Infant Behavior & Development, 21*, 201-235.

Mendes, N., & Huber, L. (2004). Object permanence in common marmosets (*Callithrix jacchus*). *Journal of Comparative Psychology, 118*(1), 103-112.

Miles, H. L. W. (1990). The cognitive foundations for reference in a signing orangutan. In S. T. Parker & K. R. Gibson (Eds.), *"Language" and intelligence in monkeys and*

apes: Comparative developmental perspectives (pp. 511-539). Cambridge, England: Cambridge Univ. Press.

Miles, H. L. W. (1994). ME CHANTEK: The development of self-awareness in a signing orangutan. In S. T. Parker, R. W. Mitchell, & M. L. Boccia (Eds.), *Self-awareness in animals and humans: Developmental perspectives* (pp. 254-272). Cambridge, England: Cambridge Univ. Press.

Milton, K. (1981). Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. *American Anthropologist, 83*, 534-548.

Milton, K. (1988). Foraging behavior and the evolution of primate intelligence. In R. W. Byrne & A. Whiten (Eds.), *Machiavellian intelligence. Social expertise and the evolution of intellect in monkeys, apes, and humans* (pp. 285-305). New York: Oxford University Press.

Moore, K. M., & Meltzoff, A. N. (1999). New findings on object permanence. A developmental difference between two types of occlusion. *British Journal of Developmental Psychology, 17*(4), 623-644.

Munakata, Y. (2001). Graded representations in behavioral dissociations. *Trends in Cognitive Sciences, 5*, 309-315.

Munakata, Y., McClelland, J. L., Johnson, M. H., & Siegler, R. S. (1997). Rethinking infant knowledge: Toward an adaptive process account of successes and failures in object permanence tasks. *Psychological Review, 104*(4), 686-713.

Natale, F. (1989). Stage 5 object-concept. In F. Antinucci F (Ed.), *Cognitive structure and development in nonhuman primates* (pp. 89-95). Hillsdale, NJ: Erlbaum.

Natale, F., Antinucci, F., Spinozzi, G., & Potí, P. (1986). Stage 6 object concept in nonhuman primate cognition: A comparison between gorilla (*Gorilla gorilla gorilla*) and Japanese macaque (*Macaca fuscata*). *Journal of Comparative Psychology, 100*, 335-339.

Neiworth, J. J., Steinmark, E., Basile B. M, Wonders, R., Steely, F., & DeHart, C. (2003). A test of object permanence in a new-world monkey species, cotton top tamarins (*Saguinus oedipus*). *Animal Cognition, 6*, 27-37.

Parker, S. T. (1977). Piaget's sensori-motor period series in an infant macaque: A model for comparing unstereotyped behavior and intelligence in human and nonhuman primates. In S. Chevalier-Skolnikoff & F. E. Poirier (Eds.), *Primate bio-social development: Biological, social and ecological determinants* (pp. 43-112). New York: Garland.

Parker, S. T., & Gibson, K. R. (1977). Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in Cebus monkeys and great apes. *Journal of Human Evolution, 6*, 623-641.

Parker, S. T., & Gibson, K. R. (1979). A developmental model for the evolution of language and intelligence in early hominids. *Behavioral and Brain Sciences, 2*, 367-408.

Pepperberg, I. M., & Funk, M. S. (1990). Object permanence in four species of psittacine birds: An African grey parrot (*Psittacus erithacus*), an Illiger mini macaw (*Ara maracana*), a parakeet (*Melopsittacus undulatus*), and a cockatiel (*Nymphicus hollandicus*). *Animal Learning & Behavior, 18,* 97–108.

Pepperberg, I. M., & Kozak, F. A. (1986). Object permanence in the African grey parrot (*Psittacus erithacus*). *Animal Learning and Behavior, 14*, 322-330.

Pepperberg, I. M. , Willner, M. R., & Gravits, L. B. (1997). Development of Piagetian object permanence in a grey parrot (*Psittacus erithacus*). *Journal of Comparative Psychology, 111*, 63-75.

Piaget, J. (1952). *The origins of intelligence in children*. (M. Cook, Trans.). New York: International University Press.

Piaget, J. (1954). *The construction of reality in the child*. (M. Cook, Trans.). New York: Basic Books. (Original work published 1937).

Pollok, B., Prior, H., & Gunturkun, O. (2000). Development of object permanence in food-storing magpies (*Pica pica*). *Journal of Comparative Psychology, 114*(2), 148-157.

Poti, P. (1989). Early sensorimotor development in macaques (*Macaca fuscata, M. fascicularis*). In F. Antinucci (Ed.), *Cognitive structure and development in nonhuman primates* (pp. 39-53). Hillsdale, NJ: L. Erlbaum Associates.

Redshaw, M. (1978). Cognitive development in human and gorilla infants. *Journal of Human Evolution, 7*, 133-141.

Ruffman, T., Slade, L., & Redman, J. (2005). Young infants' expectations about hidden objects. *Cognition, 97*, B35-B43.

Sauther, M. L., Sussman, R. W., & Gould, L. (1999). The socioecology of the ring-tailed lemur: Thirty-five years of research. *Evolutionary Anthropology, 8*(4), 120-132.

Schino, G., Spinozzi, G., & Berlinguer, L. (1990). Object concept and mental representation in *Cebus apella* and *Macaca fascicularis*. *Primates, 31*, 537-544.

Schlesinger, M., & Casey, P. (2003). Where infants look when impossible things happen: simulating and testing a gaze-direction model. *Connection Science, 15*(4), 271-280.

Schuberth, R. E. (1983). The infant's search for objects: Alternatives to Piaget's theory of concept development. In L. P. Lipsitt & C. K. Rovee-Collier (Eds.), *Advances in Infancy Research: Vol. 2* (pp. 137-182). Norwoord, NJ: Ablex.

Shinskey, J. L. (2008). The sound of darkness: why do auditory cues aid infants' search for objects hidden by darkness but not by visible occluders? *Developmental Psychology, 44*(6), 1715-1725.

Shinskey, J. L., & Munakata, Y. (2003). Are infants in the dark about hidden objects? *Developmental Science, 6*(3), 273-282.

Shinskey, J. L., & Munakata, Y. (2005). Familiarity breeds searching: Infants reverse their novelty preference when reaching for hidden objects. *Psychological Science, 16*(8), 596-600.

Shutts, K., Keen, R., & Spelke, E. S. (2006). Object boundaries influence toddlers' performance in a search task. *Developmental Science, 9*(1), 97-107.

Sophian, C. (1985). Understanding the movements of objects: Early developments in spatial cognition. *British Journal of Developmental Psychology, 3,* 321–333.

Sophian, C., & Sage, S. (1983). Developments in infants' search for displaced objects. *Journal of Experimental Child Psychology, 35,* 143–160.

Spelke, E. S. (2007). Core knowledge. *Developmental Science, 10*, 89-96.

Spelke, E. S., Breinlinger, K., Macomber, J., & Jacobson, K. (1992). Origins of knowledge. *Psychological Review, 99*, 605-632.

Spelke, E. S., & Hespos, S. (2001). Continuity, competence, and the object concept. In E. Dupoux (Ed.), *Language, brain, and cognitive development: Essays in honor of Jacques Mehler* (pp. 325-340). Cambridge, MA: MIT Press.

Spinozzi, G. (1989). Early sensorimotor development in Cebus (*Cebus apella).* In F. Antinucci (Ed.), *Cognitive structure and development in nonhuman primates* (pp. 55-66). Hillsdale, NJ: Erlbaum.

Thelen, E., Schoner, G., Scheier, C., & Smith, L. B. (2001). The dynamics of embodiment: A field theory of infant perseverative reaching. *Behavioral and Brain Sciences, 24*, 1-86.

Tomasello, M., & Call, J. (1997). *Primate cognition*. New York: Oxford University Press.

Triana, E., & Pasnak, R. (1981). Object permanence in cats and dogs. *Animal Learning and Behavior, 9*, 135-139.

Uzgiris, I. C., & Hunt, J. M. (1974). *Towards ordinal scales of psychological developments in infancy.* Illinois: University of Illinois Press.

Van Schaik, C., Fox, E., & Sitompul, A. (1996). Manufacture and use of tools in wild Sumatran orangutans. *Naturwissenschaften, 83*, 186-188.

Vasey, N. (2003). *Varecia*, ruffed lemurs. In S. M. Goodman & J. P. Benstead (Eds.), *The natural history of Madagascar*, (pp. 1332-1336). Chicago: University of Chicago Press.

Vaughter, R. M., Smotherman, W., & Ordy, J. M. (1972). Development of object permanence in the infant squirrel monkey. *Developmental Psychology, 7*, 34-38.

Watson, J. S, Gergely, G., Csanyi, V., Topal, J., Gacsi, M., & Sarkozi, Z. (2001). Distinguishing logic from association in the solution of an invisible displacement task by children and dogs: Using negation of disjunction. *Journal of Comparative Psychology, 115*, 219-226.

Watts, D. P. (1996). Comparative socio-ecology of gorillas. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 16-28). Cambridge: Cambridge University Press.

Wise, K. L., Wise, L. A., & Zimmermann, R. R. (1974). Piagetian object permanence in the infant rhesus monkey. *Developmental Psychology, 10*, 429-437.

Wood, S., Moriarty, K. M., Gardner, B. T., & Gardner, R. A. (1980). Object permanence in child and chimpanzee. *Animal Learning and Behavior, 8*, 3-9.